UNIVERSIDADE FEDERAL DOS VALES DO JEQUITINHONHA E MUCURI

Programa de Pós-Graduação em Ciência Florestal

Bruno Lopes de Faria

O PAPEL DE DISTÚRBIOS SOBRE A ESTABILIDADE DE COMUNIDADES FLORESTAIS NA AMAZÔNIA: INTEGRANDO MODELAGEM E SENSORIAMENTO REMOTO

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Orientador: Prof. Dr. André Rodrigo Rech

Coorientador: Prof. Dr. Vinícius de Lima Dantas

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BRUNO LOPES DE FARIA

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Orientador: Prof. **André Rodrigo Rech**

Coorientador: Prof. **Vinícius de Lima Dantas**

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Prof. Dr. **André Rodrigo Rech**
Documento assinado digitalmente
gov.br
Andre Rodrigo Rech
Data: 16/08/2021 15:23:25-0300
Verifique em https://verificador.iti.br

(Universidade Federal dos Vales do Jequitinhonha e Mucuri)

Prof. Dr. **Bruno Vilela de Moraes e Silva**
Documento assinado digitalmente
gov.br
Bruno Vilela de Moraes e Silva
Data: 27/07/2021 15:48:17-0300
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(Universidade Federal da Bahia)

Prof. Dr. **Emerson Delano Lopes**
Documento assinado digitalmente
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Emerson Delano Lopes
Data: 15/07/2021 17:33:35-0300
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(Instituto Federal do Norte de Minas Gerais)

Profa. Dra. **Danielle Piuzana Mucida**
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Danielle Piuzana Mucida
Data: 14/07/2021 22:19:44-0300
CPF: 870.499.376-49
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(Universidade Federal dos Vales do Jequitinhonha e Mucuri)

Prof. Dr. **Gudryan Jackson Baronio**
Documento assinado digitalmente
gov.br
Gudryan Jackson Baronio
Data: 27/07/2021 20:48:36-0300
Verifique em https://verificador.iti.br

(Universidade Federal dos Vales do Jequitinhonha e Mucuri)

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RESUMO

DE FARIA, B. L. **O papel de distúrbios sobre a estabilidade de comunidades florestais na Amazônia: integrando modelagem e sensoriamento remoto**. 2021. Tese (Ciência Florestal) – Universidade Federal dos Vales do Jequitinhonha e Mucuri, Diamantina, 2021.

As interações entre desmatamento, seca, fogo, extração de madeira e efeitos de borda têm causado incêndios florestais com alta intensidade e em extensas áreas, favorecendo a degradação florestal acelerada em grandes porções da Amazônia. Estes distúrbios aumentam direta e indiretamente a inflamabilidade da floresta. Diretamente eles promovem um microclima mais seco e reduzem a umidade do material combustível. Enquanto que indiretamente influenciam na diminuição da umidade do solo desencadeando a perda de biomassa viva, como a queda de folhas e a mortalidade de árvores, o que contribui para o aumento do material combustível. Esses efeitos diretos e indiretos podem causar incêndios florestais mais abrangentes e intensos com maior impacto nos estoques de carbono florestal da Amazônia influenciando no ciclo de carbono global. Estes processos tendem a se intensificar em cenários de mudanças climáticas sendo mais frequentes e intensos à medida que o clima global muda. Além disso, esta degradação pode expor grandes áreas de floresta à invasão por gramíneas que podem promover transições para florestas degradadas pobres em espécies e com estrutura similar a uma savana. No entanto, nossa capacidade de prever os locais na Amazônia que são mais vulneráveis a essas transições ainda é reduzida. Para este fim, expandimos e aperfeiçoamos um modelo ecossistêmico de fogo acoplado para melhor representar como a seca, as mudanças climáticas e os efeitos de borda associados ao desmatamento podem afetar a probabilidade de invasão de gramíneas após um incêndio florestal na Amazônia. Buscamos também identificar onde as retroalimentações provocadas pelas interações fogo-gramíneas podem promover a persistência de florestas degradadas com estrutura similar a uma savana, mantido pela recorrência de fogo. Em condições climáticas atuais, 14% da Amazônia é vulnerável à invasão de gramíneas, com o sudeste sendo a região mais vulnerável. Sob cenário de mudanças climáticas, até o final do século, cerca de 21% da Amazônia apresenta alta probabilidade de invasão de por gramíneas após fogo. Nossos resultados também indicam que em cerca de 3% da Amazônia (mais de 100.000 km^2), os intervalos de retorno do fogo já são mais curtos do que o tempo que seria necessário para o fechamento do dossel, implicando em um alto risco de uma mudança irreversível para uma

degradação mantida pelo fogo. Embora a resiliência na regeneração do dossel seja evidente em áreas com baixa frequência de fogo, o aumento de sua frequência pode inibir a regeneração do dossel e favorecer a aproximação de um ponto de inflexão para algumas partes da Amazônia, fazendo com que grandes áreas de floresta façam a transição para uma floresta degradada com baixa cobertura de árvores. Ademais, nossas simulações de crescimento florestal também sugerem que regiões gravemente afetadas pelos distúrbios e suas sinergias podem ter perda significativa de biomassa, levando dezenas de anos para sua recuperação integral. Os valores máximos atingem 184 anos para recompor o estoque de carbono inicial. Nosso estudo mostra como modelos, combinados com dados de sensoriamento remoto, podem ser usados como ferramentas para complementar os estudos de campo sobre a recuperação florestal, possibilitando avaliar em escalas mais largas a dinâmica espacial e temporal dos processos de recuperação florestal. Isso contribui para o planejamento, decisão e formulação de políticas de mitigação e adaptação as ameaças presentes na Amazônia atual e futuramente.

Palavras chave: Amazônia, degradação florestal, invasão de gramíneas, fogo, mudanças climáticas, modelagem,

ABSTRACT

Drought-fire interactions associated with deforestation have caused widespread Amazon Forest degradation. As climate change, this process may become more common, widespread, and intense. Amazon droughts directly increase forest flammability by increasing air dryness and reducing fuel moisture. These disturbances also increase forest flammability indirectly by decreasing soil moisture, which triggers leaf shedding, branch losses, and tree mortality – all of which contribute to increased fuel loads. These direct and indirect effects can cause widespread forest fires that reduce forest carbon stocks in the Amazon, with potentially important consequences for the global carbon cycle. These processes are expected to become more widespread, common, and intense as global climate changes, yet the mechanisms linking droughts, wildfires, and associated changes in carbon stocks remain poorly understood. In addition, this degradation may promote transitions to species-poor degraded forests with savanna-like structure. However, our ability to predict the locations in the Amazon that are most vulnerable to these transitions is limited. Here, we expanded the capabilities of a fire-ecosystem model to better represent disturbances effects on carbon and fuel dynamics, the understory fire behavior and severity. after that we combined this model with empirically derived equations and remote sensing products to evaluate how drought, climate change and deforestation could affect the probability of post-fire grass invasion across the Amazon, and identify where grass-fire feedbacks may promote the persistence of species-poor degraded forests with savanna-like structure. Under current climatic conditions, 14% of the Amazon is vulnerable to post-fire grass invasion, with the south-eastern Amazon at highest risk of invasion. We find that under unmitigated climate change, by the end of the century, 21% of the Amazon would present a high probability of post-fire grass invasion. Our results also suggest that, under current climatic conditions, 3% of the Amazon, fire return intervals are already shorter than the time that would be required for grass exclusion due to canopy recovery, implying a high risk of an irreversible shift to a fire-maintained degraded ecosystem state. Although resilience in canopy regeneration is evident in areas with low fire frequency, increased fire frequency and intensity could inhibit regeneration. This could push Amazon forests towards a tipping point, causing large areas of forest to transition to a low tree cover state. Moreover, our simulations also indicate that the regions highly affected by disturbance synergisms (i.e., the interacting effects between disturbances) may suffer a significant loss of biomass, that can take decades to fully recover, with values reaching 184 years in areas of high fire intensity. This study shows how forest growth models can be

used as tools for complementing field-based studies on recovery time by investigating the spatial and temporal dynamics and processes of forest recovery, which contributes to the planning, decision and formulation of mitigation and adaptation policies.

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Keywords: Amazon, Forest degradation, grass invasion, fire, climate change, modeling

SUMÁRIO

1 INTRODUÇÃO GERAL

Distúrbios como secas, incêndios florestais, extração de madeira e efeitos de borda associados ao desmatamento degradaram enormemente a Amazônia nos últimos 30 anos. Incêndios florestais generalizados tornam-se um novo normal em muitas partes da região, favorecidos pelo aumento das fontes de ignição relacionadas à ocupação humana e a estações secas mais longas decorrentes das mudanças climáticas (Marengo et al. 2018).

A Amazônia provavelmente terá um "ponto de inflexão" nos próximos 50-100 anos, ou seja, um limiar além do qual uma combinação de pressões humanas diretas - incêndios florestais e desmatamento, juntamente com pressões indiretas por meio das mudanças climáticas- poderiam alterar o sistema de uma floresta tropical úmida para uma floresta degradada, em um estado alternativo parecido com o de uma savana (Wuyts et al., 2017; Lenton et al., 2008/2019). Com a intensificação das mudanças climáticas e o desmatamento na Amazônia se aproximando de um quinto da área total da floresta, já existem sinais preocupantes de que este ponto de inflexão possa ser iminente (Lovejoy e Nobre, 2019), com estudos mostrando reduções recentes na precipitação (Barkhordarian et al., 2019) e até mudanças na composição da floresta nos últimos 30 anos (Esquivel-Muelbert et al., 2019).

O fogo é um elemento que promove um processo ecológico chave em ecossistemas em todo mundo, seus impactos influenciam uma ampla gama de atributos do ambiente, desde a estrutura da vegetação, a emissões/sequestro de carbono até padrões de biodiversidade em múltiplas escalas (Bowman et al. 2009). Embora os efeitos do fogo na vegetação possam ser positivos em determinados ambientes (Fidelis 2020), em áreas florestais compostas por níveis diferentes de resistência e resiliência ao fogo o impacto das queimadas pode ser devastador. Na Amazônia, por exemplo, o aumento dos incêndios florestais é preocupante. No passado, antes da presença humana, os eventos de fogo eram muito raros e ocorriam a cada 500–1000 anos; já atualmente ocorrem a cada 5–10 anos em algumas regiões (Bush et al. 2008). Esses cenários podem se intensificar ainda mais

com mudanças futuras na composição da atmosfera e enfraquecimento da governança na região. As mudanças climáticas se relacionam de maneira direta e indireta com as sinergias entre seca e fogo (Figura 1). Desde meados da década 1970 ocorre um aquecimento médio de aproximadamente 0,25 ^{o}C por década, em regiões de floresta tropical (Malhi & Wright, 2004), e projeções de modelos climáticos sugerem aumentos entre 3 e 8 °C até ao final do século, quando as temperaturas tropicais atingirão valores sem precedentes, fora da variabilidade natural dos últimos dois milhões de anos (Cramer *et al.* 2004).

Na floresta Amazônica, as mais de 8.000 espécies de árvores praticamente não têm adaptações ao fogo, e mesmo incêndios florestais de baixa intensidade podem matar mais da metade das árvores de uma área (Berenguer et al. 2021). Assim sendo, incêndios recorrentes podem até mesmo resultar em extinção de espécies (Barlow et al. 2003) e causar uma substituição lenta e gradual da vegetação atual por uma floresta seca mais tolerante ao fogo e com redução da cobertura de árvores (Silvério et al. 2013). Essa degradação da floresta retroalimenta os regimes de fogo que se tornam mais abrangentes e intensos (Brando et al., 2014) criando novos sistemas de *feedbacks* que podem conduzir comunidades inteiras para outros estados permanentes nos quais a resiliência não possa mais atuar. Em contrapartida aos ambientes florestais, áreas savânicas possuem naturalmente um dossel muito mais aberto e a ocorrência de fogo, historicamente natural, selecionou uma série de adaptações que garantem, à vegetação, a convivência e até mesmo dependência de regimes de fogo. Nesses ambientes podem ser observadas variações na espessura das cascas, promoção e quebra de dormência, perda de folhas entre outras tantas modificações da vegetação mediadas ou promovidas pela ocorrência do fogo (Fidelis, 2020).

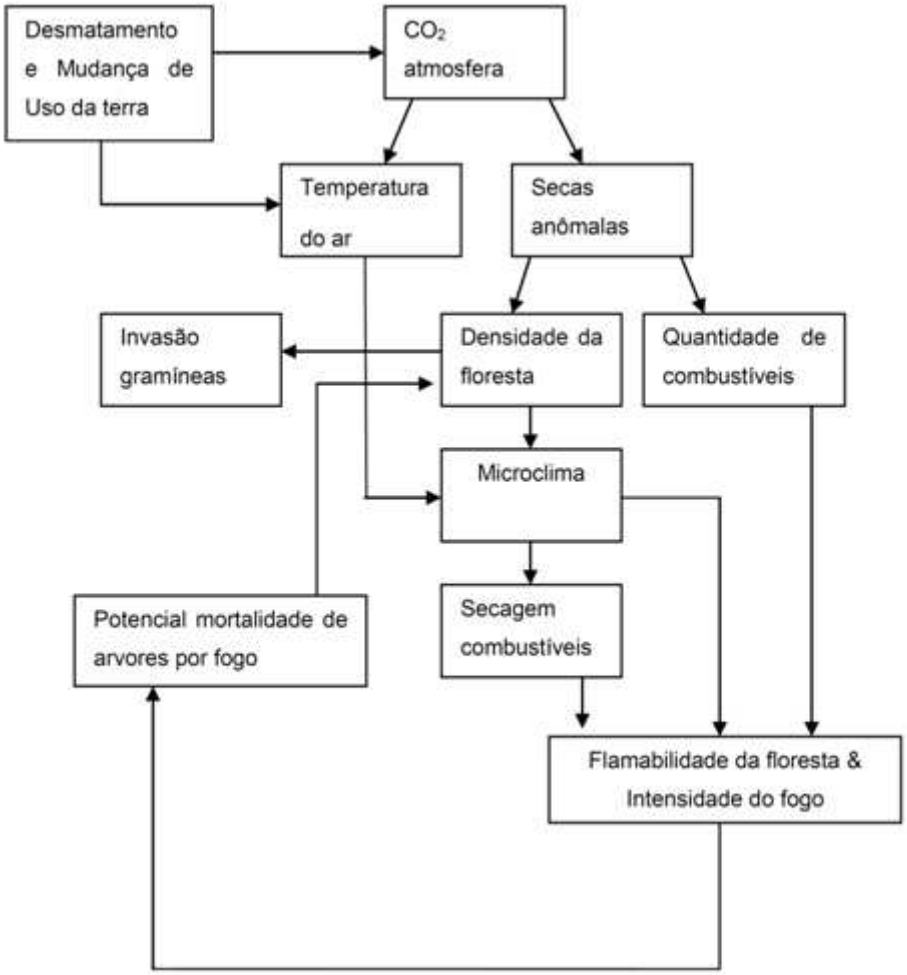

Figura 1 - Diagrama mostrando os efeitos potenciais das mudanças climáticas na dinâmica da floresta. As florestas da Amazônia estão sendo alteradas por distúrbios como secas severas, uso da terra (desmatamento, exploração madeireira) e incêndios florestais frequentes. Alguns desses processos são auto reforçados por meio de retroalimentações positivas, (ou feedbacks positivos) e podem impulsionar o sistema para um ponto de inflexão em grande escala.

As causas dos incêndios florestais são numerosas, mas a maioria está ligada direta ou indiretamente às atividades humanas, como práticas de manejo da terra associadas ao uso do fogo (e.g. limpeza de pastagens e manutenção de terras, incêndios de e para desmatamento, escape de fogo de atividades madeireiras ou até queimadas intencionais). A capacidade dos humanos no manejo do fogo e no controle de incêndios florestais ainda é reduzida e pode se tornar mais difícil no futuro com as mudanças globais, como as mudanças climáticas e de uso da terra, aliadas ao crescimento populacional e a expansão da rede de estradas que tendem a aumentar o risco de ignições de fogo (Cardoso et. al

2003). Essas mudanças alteram os regimes de fogo, fazendo com que os ecossistemas se adaptem/modifiquem ou sejam substituídos. Um exemplo do papel do fogo enquanto mediador das alterações em comunidades vegetais ocorre quando a queima induz à abertura do dossel, agindo como um forte filtro ambiental nas características do microclima do sub-bosque da floresta facilitando a invasão de espécies de gramíneas que agem como propulsores da inflamabilidade da vegetação (Figura 2). Eventualmente as espécies invasoras podem vir a dominar o sub-bosque da floresta. Algumas gramíneas exóticas, por exemplo, caracterizam-se como um conjunto de espécies invasoras notáveis por sua capacidade de alterar significativamente os ecossistemas invadidos (Kerns et al. 2020).

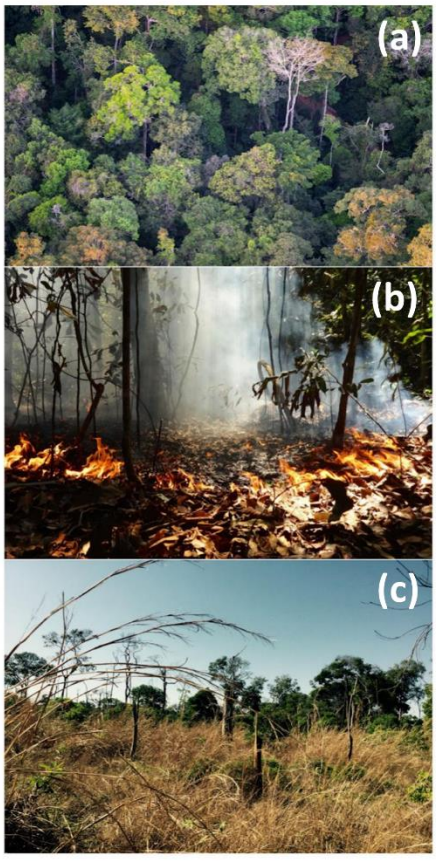

Figura 2. Estados alternativos mediados pelo fogo na região do sudeste amazônico. Floresta com dossel fechado, não queimado (a). Incêndio florestal no sub-bosque da floresta (b). Floresta invadida por gramíneas após incêndio florestal (c). Cedidas por Paulo Brando.

Assim, fica evidente que o futuro das relações entre vegetação, fogo e mudanças globais (i.e mudanças climáticas e de uso da terra) é fundamental para prever o que pode acontecer com essa região que é central para a vida no planeta (Zemp et. al 2017, Bernardino et. al 2021). Consequentemente, para entender as trajetórias futuras da vegetação, precisamos de uma síntese com questões importantes que serão abordadas, nesta tese, incluindo:

i) Existem áreas na Amazônia sob risco de sofrer mudanças irreversíveis para novos estados de ecossistemas semelhantes a savanas em resposta a incêndios florestais? Quais seus tamanhos e localizações?

ii) Como as mudanças climáticas e de uso da terra afetarão as futuras trajetórias de florestas e ambientes abertos?

iii) Quanto tempo uma floresta degradada pelo fogo demora para voltar ao estado original, antes do distúrbio?

Para responder a essas questões essa tese foi estruturada em três capítulos:

i) o primeiro faz uma revisão da literatura sobre o arcabouço teórico e metodológico da tese;

ii) No segundo capítulo, avaliamos os padrões de vulnerabilidade da floresta à presença/invasão de gramíneas para cenários pós-fogo, um processo complexo, ainda pouco compreendido e não bem representado em modelos dinâmicos de vegetação. Ademais, discutimos sobre a iminência de um *tipping point*, na Amazônia.

iii) No terceiro capítulo, avaliamos o impacto e o tempo de recuperação de eventos de seca e fogo na Amazônia, com base no tempo de recuperação dos estoques de carbono da floresta simulado pelo modelo de crescimento florestal 3-PG.

2 CAPÍTULO 1: CONTEXTUALIZAÇÃO DO ARCABOUÇO TEÓRICO E METODOLÓGICO DA TESE

2.1 O papel do fogo na estabilidade florestal

Dados paleoecológicos e de satélite sustentam a ideia de que o fogo tenha um papel importante na bi-estabilidade da vegetação tropical (Mayle; Power, 2008), por exemplo, fogo é presente nas savanas e ausente nas florestas (Bernardino et al 2021). Estes estados de vegetação alternativos ao regime (presença ou ausência) do fogo representa o conceito de bi-estabilidade (Pausas, 2015). Alguns defendem que a distribuição da floresta e da savana é determinada por envelopes climático-edáficos (Quesada et al., 2012; Veenendaal et al., 2015). Outros exploram o papel de um sistema de *feedback* positivos entre as plantas e o fogo (Cochrane et al. ,1999; Hoffmann et al., 2012; Dantas et al., 2016).

Nas savanas, a vegetação herbácea coexiste com árvores adultas, com incêndios que eliminam as árvores em processo de recrutamento (Sankaran et al., 2004; Silva et al., 2013). Esse feedback positivo aprisiona o sistema em um estado de baixa cobertura de árvores (Grady e Hoffmann, 2012). No entanto, quando o fogo é suprimido do sistema, indivíduos arboreos são capazes de recrutar (Higgins et al., 2007; Pellegrini et al., 2015), criando um sistema de feedbacks que promove o fechamento do dossel, suprimindo o fogo e excluindo gramíneas (Silva et al., 2013). Quando o fogo escapa para sub-bosques das florestas tropicais, a vegetação pode ser impactada de várias maneiras. Na Amazônia, onde o fogo é de origem antrópica, os incêndios florestais podem alterar drasticamente a composição de comunidades florestais, selecionando árvores pioneiras (Barlow e Peres, 2008), árvores com maior tolerância ao fogo (Veldman e Putz, 2011) ou com capacidade de rebrota (Jakovac et al., 2015).

No entanto, a resiliência de espécies florestais permite que o sistema recupere o fechamento do dossel em um curto espaço de tempo (Mesquita et al., 2001; Jakovac et al., 2015). Em razão da “aparente” alta resiliência das florestas amazônicas (Poorter et

al., 2016), os mecanismos que podem levar a floresta a uma transição para formações degradadas semelhantes a savanas permanecem incertos. Note que esta semelhança com savanas ocorre apenas na forma, indicando que as comunidades florestais não são mais capazes de sustentar árvores de grande porte e reter biomassa a longo prazo. Evidências sugerem que uma savana típica pode levar séculos ou até milênios para se formar (Nerlekar e Veldman 2020). Por exemplo, sob fogo recorrente, a invasão de gramíneas é limitada à borda da floresta (Silvério et al., 2013; Brando et al., 2014). Florestas perturbadas são principalmente dominadas por poucas espécies herbáceas não nativas, contrastando com a camada herbácea diversa de verdadeiras savanas (Veldman e Putz, 2011).

Quando as condições de estresse aumentam sobre as comunidades florestais, a recuperação das perturbações torna-se mais lenta, anunciando que o sistema se aproxima de um ponto de inflexão (Scheffer et al., 2009). As análises da distribuição da cobertura de árvores tropicais revelam que em regiões nas quais a precipitação média anual é menor do que 1.000 mm, a ocorrência de florestas é rara, sugerindo que esse valor possa ser um ponto de inflexão para o colapso de uma floresta (Hirota et al., 2011; Staver et al., 2011). Portanto, em geral, à medida que as condições de chuva caem em direção a esse limite, espera-se que a capacidade de recuperação da floresta diminua, aumentando a chance de que perturbações possam levar o sistema para um estado degradado savânico no qual um novo sistema de feedbacks impeça o retorno a condição florestada.

Há evidências para os neotrópicos de que a taxa de recuperação da biomassa florestal, após a perturbação humana, reduz drasticamente abaixo de 1.500 mm de precipitação anual (Poorter et al., 2016). Quando os sistemas tropicais se aproximam desse ponto crítico nas condições de chuva, as savanas já parecem ser relativamente mais estáveis do que as florestas e potencialmente mais prováveis de se expandir (Staal et al., 2016). Um mecanismo importante que poderia explicar tal expansão é um feedback entre a gramíneas e o fogo (Murphy & Bowman, 2012). Nas savanas, as gramíneas funcionam como combustível para fogo (Bond, 2008). As árvores de savana são adaptadas ao fogo, alocando recursos para o desenvolvimento de cascas grossas (Keeley et al., 2011), em contrapartida esta alocação implica em investir menos recursos em área foliar, o contrário ocorre em florestas. Já para as florestas tropicais há evidências de campo limitadas sobre a resiliência em relação às condições externas e também ambientais (van Nes et al., 2014). Jakovac et al. (2014) mostraram, por exemplo, que a recuperação da floresta desacelera

após repetidos ciclos de cultivo itinerante na região amazônica, sugerindo uma perda de resiliência pela intensificação do uso da terra. (Flores, 2016)

Embora a recuperação da floresta em sistemas tropicais pareça desacelerar com a seca e os distúrbios repetidos, evidências de degradação permanente da floresta, são raras (Cavelier et al. 1998; Sansevero et al. 2020), sugerindo uma alta capacidade de persistir no estado florestal. Evidência de mudanças anteriores na vegetação tropical sugerem que se a distribuição atual da cobertura de árvores é o resultado de mudanças de longo prazo entre floresta e savana (Hirota et al., 2011; Staver et al., 2011), a análise da dinâmica histórica da vegetação deve refletir esse padrão (Willis e Birks 2006). Nos ecótonos amazônicos, por exemplo a alternância entre a floresta e a savana ocorreram várias vezes durante os últimos milhares de anos (Mayle e Power, 2008). As florestas se expandiram durante os períodos de clima mais úmido, enquanto as savanas se expandiram em épocas de secam criando condições para a diversificação das suas respectivas biotas (Bush et al 2011, Baker et al 2020). A análise detalhada da distribuição recente da cobertura de árvores fornece outro viés, relacionado a influência humana (Hirota et al., 2011; Staver et al., 2011). Isso é especialmente importante porque as mudanças climáticas devem aumentar a frequência dos episódios de seca nas regiões tropicais (Cai et al., 2014; Lau e Kim, 2015; De Faria et al. 2017). Os modelos climáticos globais preveem que as savanas se expandirão nas fronteiras da floresta amazônica em um futuro próximo como uma resposta à mudança climática (Cox et al., 2004; Malhi et al., 2009). No entanto, dada a velocidade desses processos, essa expansão deve se dar apenas com as espécies de alta mobilidade. Tal expectativa destaca a necessidade de uma avaliação detalhada do que acontece com a resiliência da floresta tropical durante o processo que resulta na transição para formações degradadas semelhantes a savanas. (Staal, 2018; Flores, 2016, De Faria et al. 2019).

2.2 Modelagem

A complexidade dos ecossistemas terrestres, com muitas interações entre seus vários componentes, limita nossa capacidade de entender e prever padrões de respostas do sistema em escalas espaciais mais grossas (maior grão ex: escala regional ~1000s km)

com base somente em extrapolações de estatísticas simples derivadas de estudos de campo (Cuddington et al. 2013). Nessas escalas as ferramentas amplamente utilizadas para uma avaliação de modo antecipado da dinâmica da vegetação em resposta às mudanças globais (mudanças climáticas e de uso da terra) são modelos de vegetação baseados em processos (Hartig et al., 2012). Em síntese esses modelos são a representação matemática (normalmente baseada em computador) de um ou vários processos que caracterizam o funcionamento de componentes biológicos dos ecossistemas. Portanto nos ajudam a aumentar nossa compreensão de como os ecossistemas funcionam e como eles respondem às atividades humanas (Cuddington et al. 2013)

A modelagem bem-sucedida implica uma análise diligente em relação à resolução, escala e complexidade dos processos espaciais, temporais e ecológicos incluídos, onde uma simplificação confiável pode ser alcançada usando nosso entendimento do sistema. Ademais, os processos de validação e calibração são intrínsecos à criação dos modelos. Os modelos contêm variáveis e constantes que precisam ser parametrizadas com dados observados. Rykiel (1996) define calibração como "a estimativa e o ajuste dos parâmetros e constantes do modelo para melhorar a concordância entre a saída do modelo e um conjunto de dados observados". E a validação compara o resultado simulado com observações reais utilizando dados não usados no desenvolvimento do modelo como parâmetros de calibragem dele.

Ao construir um modelo, o modelador está constantemente alterando o grau de precisão, generalidade e realismo (Levins 1966). É possível não incluir todos os detalhes de um sistema e ainda assim ter uma ferramenta preditiva extremamente útil. Como pesquisadores, queremos que um determinado processo seja estudado com o maior número de abordagens possíveis, porque da análise das disparidades e congruências entre diferentes modelagens emerge uma visão com maior realismo e probabilidade de se concretizar (Figura 1- Cuddington et al. 2013).

Quando se trata de questões ambientais cujos determinantes estão em curso, quanto maior for a congruência nos modelos, mais urgente se torna a necessidade de medidas atenuantes ou capazes de alterar o curso dos fatores causais. Quando existem múltiplos modelos de mesmo poder preditivo tentando explicar um fenômeno, de maneira geral, o cientista confrontado com esse dilema deve escolher a explicação mais simples. Escolher a explicação mais simples, dentre múltiplas opções, representa um princípio

filosófico amplamente difundido em diversas áreas da ciência que chamamos de "princípio da parcimônia". Esse critério foi proposto por um filósofo inglês, Ockham no século XVII o qual dentre hipóteses formuladas sobre as mesmas evidências, defendia ser racional acreditar na mais simples (Rieppel, 2007). Entretanto o princípio da parcimônia não deve ser usado para sustentar uma crença de que a natureza é simples, a parcimônia tem seu valor na avaliação de modelos correlativos e preditivos, já que modelos mais simples são menos propensos a *overfitting* (quando o modelo se ajusta muito bem ao conjunto de dados anteriormente observado, mas se mostra ineficaz para prever novos resultados (Coelho, Diniz-Filho, & Rangel, 2019).

O mérito dos modelos simples não reside no seu poder preditivo quantitativo detalhado, mas no fato de que eles podem revelar e nos ajudar a compreender as complexidades em sistemas reais de uma forma para a qual modelos complexos podem não ser adequados (Valdes, 2011).

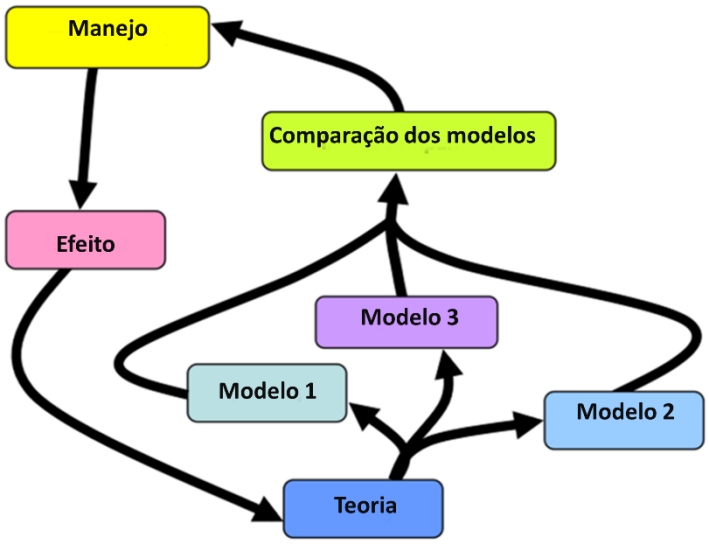

Figura 1 - Representação esquemática das relações entre teoria ecológica, modelos e manejo. Fonte: Adaptado de Cuddington et al. (2013).

Tradicionalmente, duas abordagens têm sido seguidas para entender o estado atual e futuro das florestas (Fyllas et al. 2014) bem como sua resistência à mudanças e sua resiliência. Resiliência é aqui entendida como a capacidade de um ecossistema recuperar seu estado original pré-distúrbio restabelecendo o sistema de *feedbacks* que o mantinham naquele estado de equilíbrio. (veja seção Resiliência e sistemas de *feedbacks*). No caso das florestas, uma primeira abordagem se dá por meio da análise de observações de campo de estudos de longo prazo que relacionem padrões de crescimento e mortalidade de árvores relacionados a variações climáticas e edáficas na região (e.g Esquivel-Muelbert 2019, Phillips et al., 2004; Quesada et al., 2012). Uma segunda abordagem inclui uso de modelos de vegetação dinâmicos baseados em processos, que têm sido usados para simular padrões de vegetação e fluxos de carbono na Amazônia em uma tentativa de prever o futuro da floresta amazônica (Moorcroft et al., 2001; Galbraith et al., 2010). Por exemplo, algumas projeções de modelagem sugerem perdas substanciais de carbono em cenários de mudanças climáticas (mais detalhes sobre esses cenários na seção: projeções de mudanças climáticas), com um processo rápido de empobrecimento da floresta nas próximas décadas (White et al., 1999; Cox et al., 2004) e outras simulações sugerem perdas menos aceleradas (Cramer et al., 2004) ou até mesmo ganhos (Huntingford et al., 2013).

Uma abordagem complementar às duas anteriores inclui uso de dados derivados de sensoriamento remoto (SR) que ajudam na compreensão de padrões e processos da primeira abordagem bem como na calibração e validação dos resultados da abordagem por modelagem. Por exemplo, aspectos relacionados a cobertura do dossel, tanto índice de área foliar e quanto a cobertura de árvores (derivados de SR) são comumente usados para avaliar a distribuição de floresta e savana e bem como sua resiliência em função das condições externas (Archibald et al. 2009; Staal et al. 2016). Embora os dados de satélite nos permitam avaliar um número limitado de variáveis que descrevem a vegetação e o meio ambiente, eles nos permitem avaliar padrões em largas escalas, o que não seria possível somente com dados de campo. Por não fornecerem detalhes suficientes para análises de resiliência, os dados de SR podem ser combinados em um arcabouço maior, em conjunto com modelos e equações derivadas de estudos de campo (como exemplo as análises realizadas no nosso capítulo 4). Estudos que utilizam projeções de mudanças climáticas e a modelagem de cenários futuros nos ajudam em ações de antecipação e planejamento de estratégias de mitigação das transformações nos ecossistemas. Em um mundo simplista, seria esperado que os ecossistemas respondessem de maneira linear aos distúrbios

(Scheffer et al., 2015). Entretanto, é mais comum observar mudanças abruptas entre ecossistemas se determinado limiar for ultrapassado e um novo sistema de feedbacks instalado, sugerindo que eventos de transições críticas podem ser disparados de maneira repentina se um ponto de inflexão for ultrapassado (em detalhes no tópico Resiliência e sistemas de *feedbacks*). Em relação às comunidades florestais, enquanto o desmatamento altera a capacidade das florestas de desempenhar funções básicas diminuindo sua resistência, as mudanças na estrutura e cobertura do dossel associadas a outras formas de perturbação como alterações nos regimes de fogo e efeitos de borda são mais difíceis de quantificar. Assim o aumento da intensidade e frequência de distúrbios ou mesmo a introdução de novos tipos de perturbações podem desencadear declínios não lineares e abruptos na resiliência das florestas fazendo com que os ambientes transitem para outros tipos de sistema com novos conjuntos de feedbacks que os impeçam de retornar à condição florestal (Staal, 2018).

2.3 Resiliência e sistemas de *feedbacks*

O *feedback* positivo (ou retroalimentação positiva) ocorre em todos os tipos de sistemas e é um ingrediente necessário para a presença de pontos de inflexão (Van Nes et al., 2016). Os pontos de inflexão ocorrem quando *feedbacks* positivos começam a dominar a dinâmica de um sistema e impelem o sistema para um estado estável alternativo. Uma boa maneira de ilustrar o conceito de estados estáveisalternativos é por meio de uma paisagem de estabilidade (Scheffer et al., 2001), que permite a analogia de uma bola rolando em uma superfície (Fig. 2). Sob certas condições externas (como temperatura ou precipitação), pode haver dois estados estáveis alternativos, que correspondem a mínimos locais em sua paisagem de estabilidade. Como os sistemas tendem a se mover para um estado de potencial mais baixo, o estado do sistema pode ser pensado como uma bola na paisagem que tende a se mover para o ponto local mais baixo. Um sistema com dois estados estáveisalternativos é denominado biestável.

O equilíbrio entre *feedbacks* positivos e negativos determina a resiliência de um sistema. Em geral, resiliência se refere à facilidade com que um sistema pode retornar ao seu equilíbrio (condição original) após ter sido perturbado. Dependendo da questão de

interesse, diferentes definições de resiliência podem ser apropriadas, portanto, várias definições de resiliência são encontradas na literatura (por exemplo, Walker et al., 2004; Folke, 2006).

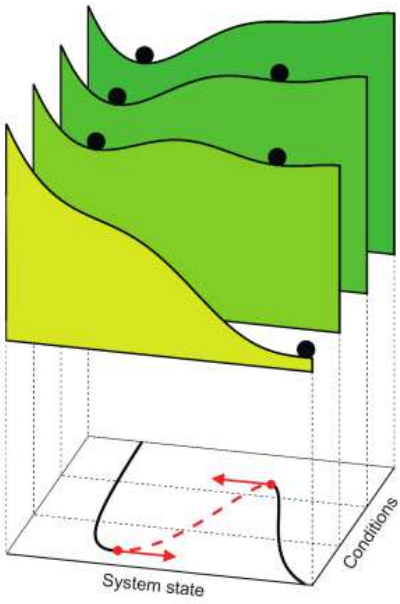

Figura 2: Um cenário de estabilidade para ilustrar o conceito de estados estáveis alternativos. No plano inferior, as linhas sólidas representam os equilíbrios estáveis do sistema e os equilíbrios instáveis da linha tracejada vermelha. Há uma série de condições (com as setas vermelhas) nas quais existem dois desses estados estáveis separados por um instável: o sistema é biestável. As paisagens no topo representam o potencial dos estados do sistema em quatro condições ambientais. Um sistema tende a se mover para um estado de potencial mais baixo, assim como uma bola tende a rolar para um ponto mais baixo na paisagem. (Fonte: Staal, 2018)

2.4 *Feedbacks* em diferentes escalas espaciais

Estudar um sistema em uma determinada escala corresponde a ter um certo ponto de vista, e manter diferentes pontos de vista pode ser necessário para obter uma imagem completa dos fenômenos de interesse. O desafio central é traduzir padrão em processo ou, em outras palavras, estática em dinâmica (Levin, 1999). Além disso, não existe uma única

escala correta ou apropriada para abordar um sistema (Levin, 1992; Holling et al., 2001). Estudar um sistema em uma determinada escala corresponde a ter um certo ponto de vista, e manter diferentes pontos de vista pode ser necessário para obter uma imagem completa dos fenômenos de interesse. Por exemplo, a relação cobertura foliar e fogo está envolvida em uma série de *feedbacks*. Incêndios florestais podem manter um estado com baixa cobertura de árvores e alta cobertura de grama: a abertura do dossel pelo fogo pode favorecer a invasão de gramíneas, que então, aumenta a inflamabilidade da floresta alimentando incêndios subsequentes. A densa cobertura de árvores aumenta as chuvas através da evapotranspiração, o que estimula o crescimento da floresta que inibe o fogo e a invasão por gramíneas. Em ambas as situações, embora os padrões finais sejam opostos, os processos para sua manutenção são dados por sistemas de *feedbacks* relacionados aos mesmos componentes do sistema.

2.5 Fogo e mudanças climáticas na Amazônia

Uma vez que as fontes de ignição estão estabelecidas e ativas, o clima passa a ter um papel fundamental na ocorrência de incêndios florestais. Algumas das variáveis climáticas mais importantes na determinação da frequência de queimadas na Amazônia são: precipitação, temperatura, umidade relativa (Cardoso et al., 2003; Sismano e Setzer, 2005), água do solo disponível para plantas (PAW) (Nepstad et al., 2004) e o déficit de pressão de vapor (VPD) dentro do dossel (Ray et al., 2005). A sazonalidade destas variáveis, que normalmente covariam, determina o período de ocorrência e intensidade (a intensidade também depende da quantidade e secagem do material combustível) do fogo na Amazônia. Na maior parte da região Amazônica, as queimadas tendem a se intensificar durante os meses de julho, agosto e setembro. Este período corresponde à estação seca com chuvas mensais abaixo de 100 mm, elevadas VPD, baixa PAW, principalmente nas partes sul e leste da Amazônia (Nepstad et al. 2011).

No entanto, este problema pode ser intensificado em condições de secas extremas como as recentemente ocorridas na Amazônia, 2005, 2007 e 2010. A maior parte das secas severas ocorridas na Amazônia está associada aos eventos de El Niños, tais como os ocorridos em 1982/1983, 1986/1987 e 1997/1998, que consistem no aquecimento das

águas do Oceano Pacífico equatorial junto a costa do Peru (Marengo, 2018). Diferentemente dos eventos citados acima, outro fenômeno tem sido apontado como causador das secas amazônicas atuais, o aquecimento da superfície das águas do Oceano Atlântico equatorial, seguindo um ciclo conhecido como Oscilação Multidecadal do Atlântico (AMO) (Li et al. 2006; Good et al., 2008; Duffy et al. 2015). Apesar de ser considerado um ciclo natural, alguns estudos indicam que este aquecimento pode estar relacionado com as mudanças climáticas globais (Cox et al., 2008). A AMO foi identificada como parcialmente responsável pela severa seca de 1997/98, e principal causadora das secas de 2005 (Marengo et al., 2008) e 2010 (Marengo et al., 2011). Essas constatações corroboram com previsões de modelos sob cenário de mudanças climáticas que indicam aumento na frequência das secas durante o século XXI. Dentre os vários impactos causados as secas severas, destaca-se o aumento da inflamabilidade das florestas e o consequente aumento na intensidade do fogo durante os incêndios florestais (Malhi et al. 2009)

2.6 Projeções de mudanças climáticas: Projeto de Intercomparação de Modelos Acoplados Fase 5 (CMIP5)

Os avanços na Ciência e na observação das mudanças climáticas estão proporcionando uma compreensão mais clara da variabilidade inerente do sistema climático da Terra e sua provável resposta às influências humanas e naturais. Os modelos climáticos globais são ferramentas fundamentais para as projeções de mudanças climáticas futuras (Knutti et al. 2013). As projeções das mudanças climáticas são incertas e a quantificação dessa incerteza é útil não apenas para o desenvolvimento de estratégias de mitigação e adaptação, bem como para a interpretação e comunicação científica (Rowell, 2012; Knutti et al. 2013). Com o advento dos Projetos de Intercomparação de Modelos Acoplados (CMIPs), uma caracterização sistemática da incerteza da projeção tornou-se possível, uma vez que uma série de modelos climáticos de complexidade semelhante forneceram simulações ao longo de um período de tempo (Knutti et al. 2013).

A necessidade de novos cenários levou o Painel Intergovernamental sobre Mudanças Climáticas (IPCC) a solicitar às comunidades científicas que desenvolvessem um novo conjunto de cenários para facilitar a avaliação futura das mudanças climáticas (IPCC 2007). O IPCC também decidiu que o desenvolvimento de novos cenários para a

comunidade científica, que propuseram o desenvolvimento de um novo conjunto de experimentos de modelos em coordenadas climáticas, que constituem a quinta fase do Coupled Model Intercomparison Project Phase 5 (CMIP5). O CMIP5, nomeadamente, vem prestando um contexto de multi-modelo para: i) avaliar os mecanismos responsáveis por diferentes modelos a entender os *feedbacks* associados com o ciclo do carbono e com as nuvens; ii) examinar "previsibilidade do clima" e explorar as capacidades de previsão de sistemas em escalas de tempo decadal e geral; e, iii) determinar por que similarmente forçantes produzem uma gama de respostas. O conjunto maior de simulações históricas e paleoclimáticas de saídas de modelos utilizados pelo CMIP5 promete oferecer novas oportunidades para uma avaliação mais detalhada sobre as projeções climáticas. Os resultados gerados pelo CMIP5 foram utilizados pelo IPCC para elaboração do 5º Relatório de Avaliação (Fifth Assessment Report - AR5) de Mudanças Climáticas (Taylor et al., 2012). A Tabela 1 apresenta a lista dos modelos do CMIP5 (Sales et al. 2015).

Tabela 1. Modelos CMIP5 – Adaptado de Sales et al. (2015)

Model Abbreviation	Model Institution and Country
bcc-csm1-1	Beijing Climate Center (BCC), China Meteorological Administration (CMA), China
BNU-ESM	College of Global Change and Earth System Science (GCESS), Beijing Normal University (BNU), China
CanAM4	Canadian Centre for Climate Modelling and Analysis (CCCma), Canada
CCSM4	National Center for Atmospheric Research (NCAR), USA
CESM1-CAM5	National Science Foundation (NSF), Department of Energy (DOE), National Center for Atmospheric Research (NCAR), USA
EC-EARTH	EC-EARTH consortium, Europe
inmcm4	Institute for Numerical Mathematics (INM), Russia

NorESM1-M	Norwegian Climate Centre (NCC), Norway
ACCESS1-0, ACCESS1-3	Commonwealth Scientific and Industrial Research Organisation (CSIRO), Australia, and Bureau of Meteorology (BOM), Australia
CMCC-CM	Centro Euro-Mediterraneo per I Cambiamenti Climatici (CMCC), Italy
CNRM-CM5	Centre National de Recherches Meteorologiques (CNRM), Centre Europeen de Recherche et Formation Avancees en Calcul Scientifique (CERFACS), France
CSIRO-Mk3-6-0	Commonwealth Scientific and Industrial Research Organisation (CSIRO) in collaboration with the Queensland Climate Change Centre of Excellence (QCCCE), Australia
FGOALS-g2, FGOALS-s2	The State Key Laboratory of Numerical Modeling for Atmospheric Sciences and Geophysical Fluid Dynamics (LASG), Institute of Atmospheric Physics (IAP), China
GFDL-CM3, GFDL-HIRAM-C180	Geophysical Fluid Dynamics Laboratory (GFDL), USA
GISS-E2-R	NASA Goddard Institute for Space Studies (GISS), USA
HadGEM2-A	Met Office Hadley Centre (MOHC), UK
IPSL-CM5A-LR, IPSL-CM5A-MR, IPSL-CM5B-LR	Institut Pierre-Simon Laplac (IPSL), France
MIROC5	Japan Agency for Marine-Earth Science and Technology (JAMSTEC), Atmosphere and Ocean Research Institute (AORI) (The University of Tokyo), and National Institute for Environmental Studies (NIES), Japan

MPI-ESM-LR, MPI-ESM-MR	Max Planck Institute for Meteorology (MPI-M), Germany
MRI-AGCM3-2H, MRI-AGCM3-2S, MRI-CGCM3	Meteorological Research Institute (MRI), Japan

O CMIP5 é a base do sucesso das fases anteriores do CMIP (Taylor et al., 2012). Na fase 3, com o CMIP3, foram realizados experimentos com um conjunto de multi-modelos fornecendo conteúdo para centenas de artigos revisados por pares, e dando os subsídios necessários para a elaboração do Relatório AR4 do Painel Intergovernamental de Mudanças Climáticas (IPCC AR4). Durante a fase 4 do CMIP, simulações adicionais foram realizadas para separar as influências antrópicas e naturais do clima do século XX (Taylor et al., 2012).

Basicamente, esse conjunto de projeções futuras (representative concentration pathways-RCPs) é dividido em cenários de emissões, baseado em projeções de crescimento populacional, forçantes radiativas e consequente aumento na temperatura, (Van Vuuren. et. al 2010) (Figura 3 – Fuss et al 2014).

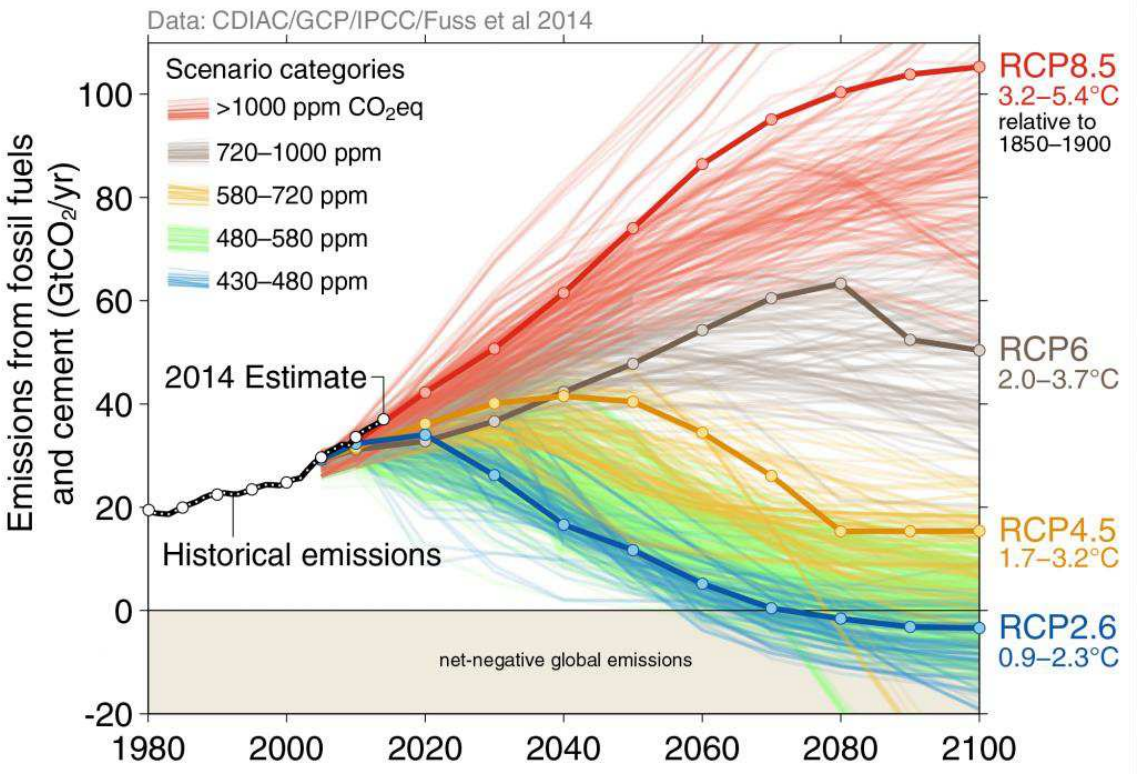

Figura 3- Mudança de temperatura global em relação a 1986-2006 para os cenários RCP executados pelos modelos do CMIP5

No momento atual a humanidade tem enfrentado uma crise climática sem precedentes, com intensificação dos distúrbios nas florestas tropicais, em especial na Amazônia, cenário que ameaça os enormes estoques de carbono presentes na floresta. Distúrbios mais frequentes e intensos podem emitir o carbono armazenado na floresta, que equivale a dez anos das atuais emissões globais de carbono por combustível fóssil. As projeções de mudanças climáticas incorporadas nas análises desta tese nos permitem uma avaliação por antecipação do papel dos impactos da amplificação dos distúrbios pelas mudanças climáticas nas comunidades florestais.

3 CHAPTER 2 - Climate Change and Deforestation Increase the Vulnerability of Amazonian Forests to Post-Fire Grass Invasion

Under review in Global Ecology and Biogeography (Impact Factor: 6.446)

ABSTRACT

Aim: The overall goal of this study is to evaluate the vulnerability of the Amazon forest to post-fire exotic grass invasion under present and future climate scenarios.

Location: Amazon basin.

Time period: 1980-2017 and 2070-2099.

Major taxa studied: Plants

Methods: We combined a fire-ecosystem model with empirically derived equations and remote sensing products to evaluate the effects of a high-intensity fire (fire during extreme drought) in canopy and grass cover under present and unmitigated climate change scenarios, on a background of logging in forest edges. We also contrasted simulated vegetation recovery time (as a function of climate) and current fire return intervals to identify areas in which the current fire frequency would suffice to lock the system in a grass-dominated state.

Results: Under current climatic conditions, 14% of the Amazon is vulnerable to post-fire grass invasion, with the south-eastern Amazon at highest risk of invasion. We find that under unmitigated climate change, by the end of the century, 21% of the Amazon would present a high probability of post-fire grass invasion. In 3% of the Amazon, fire return intervals are already shorter than the time that would be required for grass exclusion due to canopy recovery, implying a high risk of an irreversible shift to a fire-maintained degraded ecosystem state.

Main conclusions: Southeastern region of the Amazon is currently at the highest risk of irreversible degradation. Although resilience is evident in areas with low fire activity, increased fire frequency and intensity could push large Amazon forests areas towards a tipping point, causing a transition to low tree cover states.

1. Introduction

Tropical forests contain between half and two thirds of terrestrial global biodiversity and provide vital ecosystem services at local, regional, and global scales (Dixon et al. 1994; Foley et al. 2007; Marengo et al. 2018). However, these forests are undergoing widespread loss and fragmentation as a result of deforestation, climate change and fire (Hansen et al. 2013; Esquivel-Muelbert et al. 2019; Silva et al. 2020). While land cover changes impose the highest threat to tropical forests (Barlow et al. 2016), remnant forest areas are also experiencing degradation, with forests in the tropics being especially sensitive to such changes, particularly fire (Barlow and Peres 2008; Staver, et al. 2019). Modeling (Van Nes et al. 2018), observational (Hirota et al. 2011; Dantas, et al. 2013/2016) and experimental (Silverio et al. 2013) studies suggest that a positive feedback between canopy cover loss and fire may cause a shift from closed canopy forest to a grass-dominated ecosystem at the local scale upon the invasion of grasses. In the Amazon, this process seems to be especially associated with high intensity forest fires from a variety of sources occurring during exceptionally dry years, when fires can spread for hundreds of kilometers into forests (Brando et al. 2014; Withey et al. 2018). However, it is unclear the extent to which high intensity fires can affect large forest regions, such as the Amazon. Although structurally these novel grassy ecosystems can resemble savannas, they are likely to present different species composition. These novel ecosystems generally contain fewer species, and especially fewer endemic species, than both ancient savanna and forest (Veldman & Putz 2011; Veldman et al. 2015). Evidence suggests that the diversity typical of old growth savannas can take centuries or even millennia to build up (Nerlekar and Veldman 2020).

The probability of these ecosystem transitions primarily depends on the ability of grasses, especially highly flammable invasive species, to colonize forested areas. Most of those grasses are shade-intolerant and studies suggest that, as long as dispersal or moisture is not limiting, these species are mostly limited by shade (Hofmann et al. 2012; Silvério et al. 2013, Cardoso et al. 2018). In fact, studies in both Africa and South America have identified a Leaf Area Index (LAI) of 3 as the critical canopy cover threshold below which

shade-intolerant C4 grasses can spread in the forest understory (Hoffmann et al. 2012, Cardoso et al. 2018). Thus, any perturbation that reduces canopy cover below this level, such as fire or logging, may create suitable conditions for grass invasion and, possibly, grass-fire feedback to initiate (Silvério et al. 2013). Grass invasion also depends on the ability of flammable grasses dispersing to recently opened areas. The Amazon region has an ancient relationship with grasses, as these species have been present for millennia in the region (Kirschner and Hoorn 2019). However, in upland forests, flammable grass abundance appears to be higher in degraded forests near pastures and roads (Nepstad et al. 2008; Macedo et al 2011), as roads and vehicles are sources for invasive grass propagules into the forest interior over relatively long distances (Veldman & Putz 2010, 2011). While some short-term studies (< 10 years) have found grass invasion up to 250m from forest edges (Balch et al. 2015), it is unlikely that these reflect dispersal limitation, as evidence suggests that, over time, invasive grasses can be found up to 30 km from logging areas (Veldman & Putz 2010).

Fire intensity is a fundamental aspect mediating the impacts of fires on forest canopy cover. Fire intensity determines tree mortality and biomass consumption in a fire event, and a single high-intensity fire can cause enormous damage to above-ground biomass in tropical forests (Barlow et al. 2003; Brando et al. 2014). Fire intensity is largely controlled by climate and its effects on litter fuel moisture and availability. By decreasing rainfall amounts and increasing temperatures (and, thus, increasing the availability of dry litter fuels), climate change is predicted to promote fires of higher intensities in some forest regions, as drought becomes more pronounced (e.g., the southeastern portion of the Amazon basin) (De Faria et al. 2017). This would amplify the effects of fire on canopy cover, potentially increasing the extent of forest areas subject to grass invasion. In addition to fire, logging within forest edges can also facilitate grass invasion. Evidence suggests that canopy cover can be reduced by up to 60% in areas within 3 km of a forest edge (Pereira et al. 2002; Wuyts et al. 2017). The combination of high-intensity fires and logging could substantially increase the extent of areas invaded by exotic grasses in the future.

Once grasses have invaded the understory, both fire intensity and frequency may increase abruptly, as high cover of low bulk density grass fuels in the understory

dramatically increases fuel flammability (Hoffmann et al. 2011). To avoid being arrested in this 'fire trap' (Grady & Hoffman 2012; Trauernicht et al. 2016), the forest must be sufficiently resilient, that is, it must recover canopy cover quickly enough to exclude shade-intolerant flammable grasses before the next fire (Hoffmann et al. 2012). Because the growth rate of trees (at a regional scale) depends mainly on climate and moisture availability, the resilience of the forest is also dependent on how future climate will affect forest recovery rates in relation to the length of fire intervals in different parts of the forest.

One forest region that may face the threat of shifting towards a grass-invaded system is the Amazon. This threat is partially driven by a recent sharp increase in fire frequency (from once every 500–1000 years prior to modern-day human colonization, to once every 5-10 years; Bush et al. 2008), due to increasing sources of fire ignition, deforestation and climate change (Balch et al. 2015; Fearnside 2013; Gutiérrez-Vélez et al. 2014). The prevailing view is that natural fires are very rare in the region, in such way that recent fires (post-european colonization of the Americas) are generally associated to the presence of man, despite that climate probably plays a role in the severity of these fires (Bush et al. 2008). As fire activity increases the probability that a fire coincides with an extreme drought, producing forest fire events, also increases.

In this study, we combined remote sensing data, present and future climate projection, empirical equations and the ecosystem fire model CARLUC-Fire to simulate fire impacts on forest areas, their vulnerability to grass invasion and the reversibility of this process. This model has been previously used to successfully simulate fire behaviour in the Amazon (De Faria et al. 2017,2021; Brando et al. 2020). We determined the vulnerability of the Amazon basin to grass invasion by combining this model output (converted to post-fire canopy cover losses) with canopy cover losses due to logging, and empirical equations relating forest canopy cover and the probability of grass invasion (from Silvério et al. 2013), as well as exotic grass propagule dispersal limitation (using information on distance from roads).We also evaluate the reversibility of grass invasion in relation to present fire frequency by contrasting simulated vegetation recovery time (as a function of climate and predicted increases in atmospheric CO_2) and comparing it with fire return intervals. Using this framework, we addressed the following questions: i) Are there large areas in the Amazon under threat of grass invasion and irreversible shifts to novel grass-dominated ecosystem states in response to fire? ii) Where in the Amazon are the most

vulnerable areas concentrated? iii) How will climate change and the expansion of the road network affect these patterns?

We hypothesized that the already drier climate and high logging rates in the south-eastern Amazon (Silva-Junior et al. 2018) would result in the highest probability of grass invasion and ecosystem shifts under present conditions, especially near roads. Since this same region is predicted to experience increases in temperature and decreases in precipitation under climate change (Chen et al. 2011; De Faria et al. 2017; Phillips et al. 2009), we hypothesized that grass invasion will largely increase in the region under climate change, potentially undermining forest resilience to state shifts in some areas. We also expected that projected expansions in the road network would contribute to grass invasion nearby roads across the basin.

2. Material and Methods

3.1.1 Study Region

Our study focused on Amazônia *sensu stricto* in South American (Eva & Huber 2005), which contains approximately 5.5 million km^2 of tropical forest. As our main interest was on the effect of climate change and logging on forest remnant areas, we excluded deforested areas from analyses. We also excluded wetland areas, as most of our assumptions and equations were derived from studies on upland Amazon forests, which have different patterns of structure and functioning compared to floodplain forest (Flores et al. 2017). Deforested areas were determined using deforestation maps from the annual Landsat-based Project for Monitoring Amazonian Deforestation (PRODES; INPE, 2017), whereas the wetland mask generated by Hess et al. (2015) was used to exclude floodplain forests.

3.1.2 Summary of the analytical framework

To investigate forest resilience to post-fire grass invasion, under both current climate and unmitigated climate change, a framework combining remote sensing, fire-ecosystem modelling and empirically derived equations from a fire experiment study was developed. The methodological workflow used for this study is summarized in Figure 1.

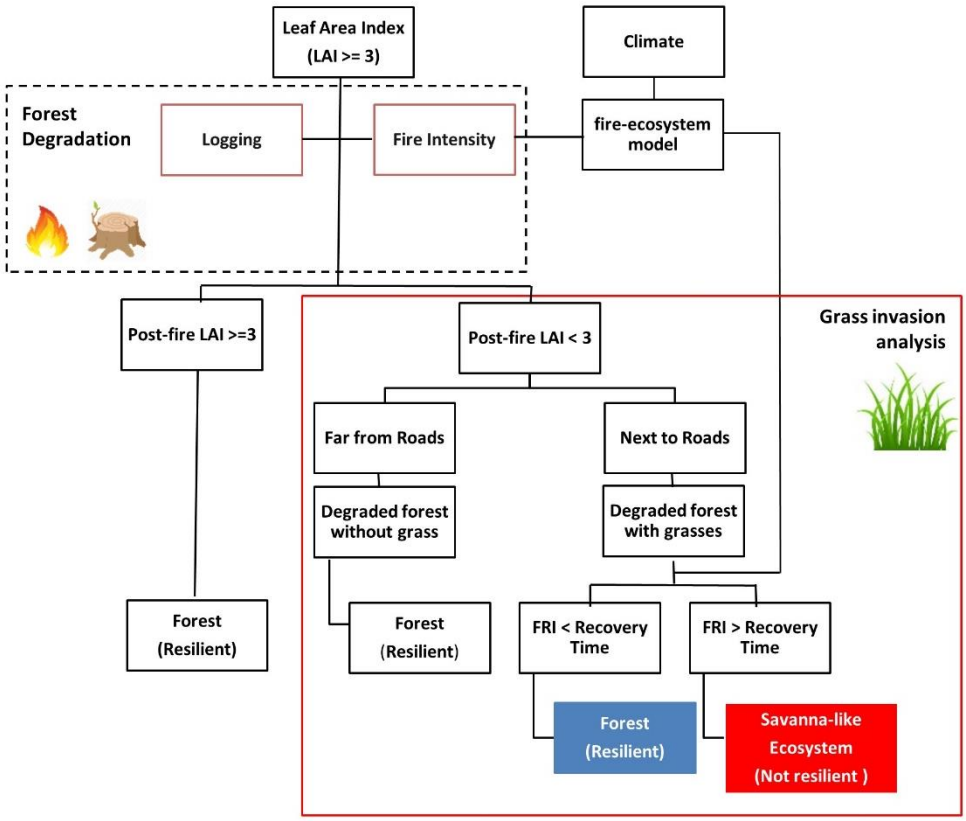

Figure 1 - Diagram of our framework that combines remote sensing (MODIS - LAI & Fire Return Interval - FRI) and the fire-ecosystem model (CARLUC-Fire) to map Amazonia-wide risk to post-fire grass invasion. CARLUC-Fire: Simulates how climate affects fire intensity, under current and future conditions as well as simulates forest recover time to reach LAI = 3.

2.2.1 Model description

To simulate canopy cover losses in terms of leaf area index (LAI) following a fire, we used the CARLUC-Fire model (De Faria et al. 2017). The model is a modified version of the Carbon and Land Use Change dynamic carbon model CARLUC (Hirsch et al. 2004). CARLUC is a process-based model of forest growth and the C cycle, driven by four monthly climatic variables: photosynthetically active radiation (PAR, mol m^{-2} $month^{-1}$), vapor pressure deficit (VPD, KPa), precipitation (mm $month^{-1}$) and mean monthly air temperature (°C), respectively, to estimate net primary productivity (NPP) and the relative changes in C-biomass stocks, as well as litter, woody debris, and humus (Hirsch et al. 2004). CARLUC-Fire is a modification of this model that combines the

resulting litter biomass component with climatic conditions to simulate fire intensity (variable across the Amazon) under specified extreme drought (e.g., a deficit of -40 mm in relation to the mean maximum climatological water deficit (defined below) conditions, based on litter amount and moisture). Fire intensity (FI, $kW \cdot m^{-1}$) measures the rate of energy released along the fire front, and is strongly correlated with the above-ground impacts of fire.

The model was calibrated and evaluated for the southern Amazon using data from a large-scale fire experiment, prescribing experimental fires from 2004 to 2010 in forest areas (Brando et al. 2014; De Faria et al. 2017). In the model, the intensity of a fire depends on fire spread rate (FSR, $m \cdot min^{-1}$) and the mass of fuel consumed by fire (W, $kg \cdot m^{-1}$). Both FSR and W depend on litter moisture content (LMC, %), while the latter (W) is also a function of load mass (Table S1; Figure S1). Fuel conditions and loads and, thus, fire intensity are influenced by climate because the maximum climatological water deficit (MCWD) is set to -40 in relation to the mean climatic condition of the grid cell, simulating drought conditions whose severity directly depends on climate. MCWD is defined as the annual cumulative difference between precipitation and mean regionwide evapotranspiration. Under these conditions, fuel moisture declines linearly with increasing temperature and vapor pressure deficit (VPD; Ray et al. 2005), while fuel amounts increase with water stress represented by maximum climatological water deficit (MCWD) (Eq. S1).

The relationship between MCWD and changes in biomass (Phillips et al. 2009) was derived from the Amazon forest inventory network (RAINFOR): when difference in the MCWD in relation to the time series mean MCWD drops below −40 mmleaf and branch shedding occurs as linear function of MCWD transferring part of the live carbon stocks to litter material. Increasing the fuel loads leads to increasing fire intensity. Given that fire intensity and damage to above-ground biomass are highly correlated in tropical forests (Brando et al. 2012, 2014), especially regarding fire-induced tree mortality (i.e., biomass turnover) in woody plants (Higgins, Bond & Trollope 2000), a high fire intensity implies larger canopy cover losses. Based on fire experiments relating fire intensity and fire-induced biomass losses (Brando et al. 2014; De Faria et al. 2017) (Eq. 1), in which the relationship showed an adjusted R^2 of 0.98, CARLUC-Fire can be used to calculate the percentage of the Aboveground Biomass (AGB) that is lost as:

$$Percent\ loss\ of\ ABG\ = \frac{1}{1 + exp(2.45 - 0.002373 * FI)}$$ (Eq. 1)

The percent loss of ABG is provided by the model as leaf, branch and stem components. ABG leaf losses can be converted to LAI losses by multiplying it by a specific leaf area (the fresh area of a leaf divided by its total mass) value of 20 $m^2.kg^{-1}$, following Hirsch et al. (2004). The LAI losses can then be subtracted from the initial (pre-fire) LAI.

2.2.3 Grass invasion modeling and forest resilience assessment

To understand how a fire event could affect the probability of grass invasion, under present (1980-2017) and future conditions (2070-2099), we calculated post-fire Leaf Area Index losses as a function of climatic conditions using the CARLUC-fire model. This loss was then subtracted from the pre-fire LAI under present (observed MODIS LAI data) and future (simulated LAI data) climatic conditions(see details in "Pre-fire canopy cover"below). We then compared the results with and without imposing an additional loss of 60% in forest edge areas (based on literature information; Pereira et al. 2002) to simulate the additional effect of logging. The final LAI was used to calculate the probability of grass using an empirical equation from fire experiments in the southern Amazon. Areas that were far from roads (>30 km) were masked out to account for the dispersal limitation of exotic grass species (Veldman & Putz 2010). Finally, we evaluated the reversibility of grass invasion in relation to present fire return interval by comparing the pixel-level (3 × 3 km) time required for an invaded forest pixel to recover a LAI value of 3 (empirically estimated as the value separating areas with high and low probabilities of grass invasion (Hoffmann et al. 2012)) and compared this lag with pixel-level fire return intervals from a MODIS product (MDC64A1; Giglio et al. 2018). The forest canopy recovery time was also simulated using the CARLUC-Fire model.

2.2.3 Pre-fire canopy cover

While the CARLUC-fire model can be used to simulate LAI based on climatic conditions, to reduce model error we set the initial pre-fire LAI to 2010 estimates of the MODIS-derived LAI product (MCD15A2H; Myneni et al. 2015). to minimize model uncertainties. Because under future climate conditions the vegetation potential is likely to

change, we implemented a correction in the present LAI values in order to account for these potential changes. Specifically, for the future conditions, we added the pixel level differences in productivity between present and future climates, as simulated by the CARLUC-Fire model, therefore, accounting for potential changes in vegetation productivity. The correction term was calculated by (1) simulating present and future leaf biomass using the CARLUC model; (2) multiplying these values by SLA to obtain LAI; (3) calculating the difference between the estimated LAI for future and present condition mediated by differences in plant productivity resulting from climate change; and (4) summing the difference to the MODIS LAI values. This was targeted at improving the realism of our results in relation to purely simulated LAI values. While these remote sensing products generally do not capture understory vegetation structure accurately, field data suggest that, in the field, the LAI of the upper stratum is a fairly accurate predictor of the total LAI of a tropical forest stand (see Fig. S2).

2.2.4 Fire effects on forest canopy cover

To estimate the resulting canopy cover after a fire for present and future climatic conditions we run the fire component of the CARLUC-fire model with two scenarios: one for current climate conditions and one for unmitigated predictions for climate change (2070-2099). For current conditions we ran the model using mean climate conditions for 1980-2017, calculated using monthly series of temperature and vapor pressure from the Climatic Research Unit dataset (CRU TS; Harris et al., 2014) and precipitation (related with water stress, MCWD) from NASA's Tropical Rainfall Measurement Mission (TRMM, data product 3B43).

For the unmitigated climate change scenario, we used climatic conditions averaged air temperature and precipitation projections from all 35 climate models participating in the Coupled Model Intercomparison Project Phase 5 (CMIP5) to adapt the biomass loss terms in CARLUC-Fire. Specifically, we used a scenario for 2070-2099 based on a Representative Concentration Pathways (RCP8.5, representing unmitigated climate changes scenario). This scenario assumes a continued increase in greenhouse gas emissions, leading to air temperature increasing by approximately 4-5°C across the southern Amazon, and reduced precipitation during the dry season (Duffy et al. 2015; De Faria et

al. 2017; Phillips et al. 2009). The climatic variables, air temperature data (related with air dryness, VPD) and precipitation (related with water stress, MCWD) from 2070–2099 were evaluated and bias-corrected (corrects the projected/simulate output using the differences in the mean and variability between simulations and observations) with the observed data (CRU and TRMM). In details, projected temperature and precipitation were corrected for 1980-2009 using CRU (TS, v.3.22) and TRMM (product 3B43) respectively. The future VPD was derived from the variation of monthly air temperatures (ΔT between historical and future simulations) and then modeled the future vapor saturation pressure (es) as a function of ΔT ($\Delta es(T)=0.611\ exp(17.21\Delta T\Delta T+237.3)$) and the vapor pressure was kept constant. As VPD is equal to vapor pressure (saturation) minus vapor pressure (air), increase in vapor saturation pressure implies an increase in VPD.

2.2.4 Logging impacts on forest canopy cover

In addition to the climate-change-mediated effects of fire on LAI, we also analyzed the impact of logging on canopy cover losses. Evidence suggests that logging occurs up to 2-3 km from the forest border, and, alone, can reduce canopy cover by 10-60 % (Pereira et al. 2002, Wuyts et al. 2017). Thus, to simulate the effects of logging on forest edges, we imposed an additional 60% LAI loss (a worst-case scenario) in the post-fire LAI in areas ≤3 km from the forest border. We also did a sensitivity analysis using the lower projected losses (10%). Deforestation areas were used to define forest borders All paving and projected roads were also included as forest edges. Distances to edges were performed using R (R Development Core Team, 2012) and QGIS. Edge distances were not updated after applying fire-induced losses, that is, degraded forests were still considered as part of the remnant forest.

2.2.5 Post-fire grass invasion analysis

Under our approach, grass invasion is assumed to dependent basically on two factors, light availability and dispersal limitation. We used an empirically derived equation (Eq. S2; Fig. S1) relating LAI and the probability of grass invasion from Silverio et al. (2013) to evaluate grass invasion in each 3 × 3 km pixel after fire- and logging- induced canopy cover losses.

In addition to canopy cover, grass invasion also depends on the availability of grass propagule sources. To incorporate dispersal limitation of exotic grass species we masked out areas that were too far from roads (>30 km; Veldman & Putz 2010) to make

sure that only areas with sufficient exotic grass propagules were considered. We used the present road network (including unpaved roads in the whole basin (Figure S4) for the analyses under present climatic conditions and the projected future network (from Department of Transport Infrastructure (DNIT) (http://servicos.dnit.gov.br/vgeo/)) for the analyses under future climatic conditions.

In the context of this study, we are considering invasion by any grass species, but especially exotic species, which are often perennial (D'Antonio et al. 2001, Silvério et al. 2013, Veldman & Putz 2010, Zenni & Ziller 2011). In general, perennial species have late germination and low seed production, but invasive species can invest substantial resources in reproduction and have high germination rates even when environmental resources are limited (Pysek and Richardson, 2008). Invasive species in the regions includes the African *Melinis minutiflora* (Zenni & Ziller 2011). This species was shown to produce more 2000 seeds/m^2. Another important invasive species is *Urochloa decumbens* (Silvério et al. 2013). The seeds of both species are fire resistant and are often found distant from parent plants (D'Antonio et al. 2001; Gorgone-Barbosa et al. 2016; Dairel & Fidelis 2020). Evidence suggests that *Urochloa decumbens* could show seed dormancy in response to temperature variation (Gorgone-Barbosa et al. 2016; Dairel & Fidelis 2020). Here we assume that no grass species are able to compete with trees and that grasses are solely limited by light availability and dispersal limitation.

2.2.6 Forest resilience analyses

To identify locations that may be under extreme threat of being trapped in a grass-fire feedback loop we compared the time required for each pixel to recover a LAI value of 3 (thereby allowing for the exclusion of grasses) with the observed satellite-derived mean fire interval between 2003-2016. A LAI of 3 represents approximately the inflection point of the logistic model relating LAI and grass invasion probability (see Eq S2; Fig. S3). Thus, at this point, small changes in LAI can quickly drive the system from one state (lightly invaded) to the other (substantially invaded; Figure S3). Because the forest continues to lose tree cover during several months after a fire (Brando et al. 2019), it is very likely that a transition to a savanna-like state would occur if, immediately after a fire, LAI drops to 3. Previous studies in moist savanna-forest regions of South America and Africa

confirm this critical value (Hoffmann et al. 2012, Cardoso et al. 2018). Here, this threshold represents a probability of grass invasion 30 %.

LAI recovery time was calculated as a function of our climate input variables using equations for forest productivity in the CARLUC model (Hirsch et al. 2004). These equations were calibrated for the Amazon and were shown to predict recovery 20 years after mid to severe disturbances fairly well, despite that the model does not explicitly consider resprouting (Hirsch et al. 2004; overall model parameters description and error terms are shown Table S2). Here we assume that our high intensity fires alone and coupled with deforestation represent mid to severe disturbances and, therefore, we expect the model to perform well in simulating forest recovery after these events. We considered a forest area to be resilient when the time required to achieve an LAI of 3 was shorter than or equal to the current mean fire interval of the area, and non-resilient otherwise. Fire return interval per pixel (FRI) was calculated using MODIS Burned Area Product Collection 6 (MDC64A1; Giglio et al. 2018) and The Global Fire Atlas dataset (Andela et al. 2019). FRI was calculated from the ignition frequency for the 13-year period 2003-2016 and was determined as the inverse of fire frequency. Based on observations for forests and savannas occurring in the same climate (Dantas et al. 2016), we reduced the mean fire interval by 50% in areas where LAI values drop below 3 following a fire and that were near to forest edge. We did not model changes in FRI resulting from climate change because the relationship between fire probability and climate in South America is non-linear (e.g., Lehmann et al. 2011) and, in the Amazon, is greatly influenced by anthropogenic ignitions, generating much uncertainty in the exact location of fires. Moreover, we did not consider the effect of CO_2 fertilization on recovery rates because these effects are uncertain (van der Sleen et al. 2014; Walker et al. 2020) given the nutrient limited nature of tropical soils (Ellsworth et al. 2017).

3.2 Results

We found that 338,702 km^2, that is, approximately 6% of the total forest area (Fig. 2a), has a high probability of grass invasion following a fire under the current climate (1980-2017). Under unmitigated climate change, the total area with high probability of grass invasion would increase to 526,358 km^2 by the end of the century (2070-2099), a 60% rise (Fig. 2b). This area would amount to 10% of the Amazon and imply large changes in the frequency distribution of LAI under climate change compared to present

conditions due to shifts in local forest LAI towards lower values (Fig. 3). Climate change alone had a very subtle effect on forest productivity as simulated in future climate conditions (Fig. 3b), and, thus, the changes under climate change were mainly explained by changes in fire intensity. In both present and future conditions, we found that the southeastern part and, on a smaller scale, the southwestern part of the Brazilian Amazon (Acre state), would be the most severely affected areas (Fig. 2b).

Approximately 511,778 km^2 of forest patches were within 3 km from a forest edge, in human influence zones (Fig. 2a1). Most of these areas are located near roads in the southeastern Amazon, particularly the Xingu river headwaters and across the "arc of deforestation" in Brazil. Accounting for edge effects (logging) resulted in an increase in the areas under high risk of grass invasion by 240 %, totalizing 809,849 km^2 under current conditions (about 14% of the Amazon region) (Fig. 2a1) and 1.15 million km^2, 21% of the region, under and future conditions, when considering both increased fire intensity and edge effects (Fig. 2b1). Even in case of the more conservative scenario in which canopy cover losses in edge areas were only 10 % (instead of the assumed 60 %, i.e., a worst-case scenario; Pereira et al. 2002), areas under high risk of grass invasion would still totalize 499,288 km^2 (an increase by 50 %) and 689,154 km^2 under current and future conditions, respectively.

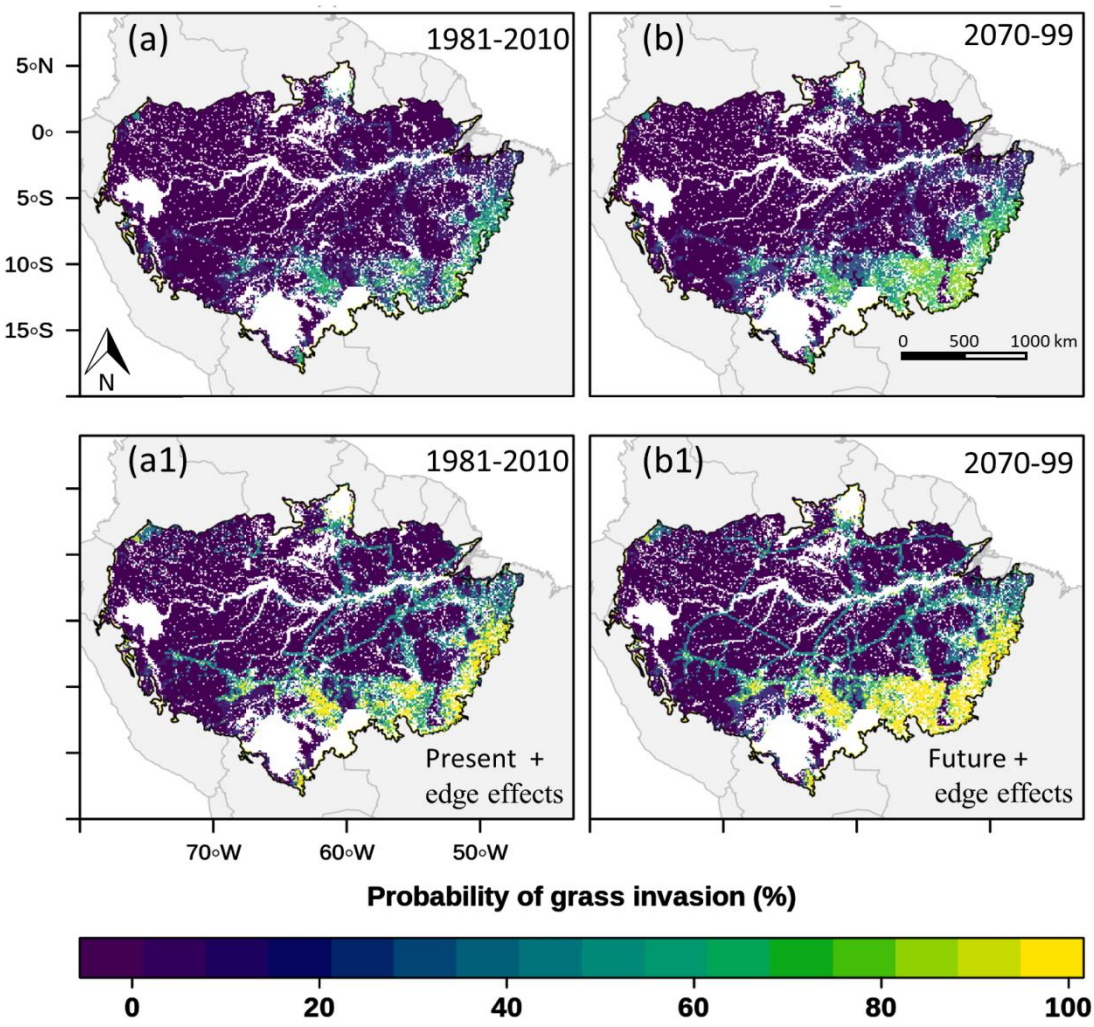

Figure 2 - Probability of grass invasion (%) after fire, calculated based on post-fire Leaf Area Index and deforestation resulting from logging in forest edge areas. (a) The probability of grass invasion under current (1980-2017) climate conditions. (b) The probability of grass invasion under average conditions projected for 2070-2099, in an unmitigated climate change scenario. (a1-b1) The probability of grass invasion after fire in a and b, respectively, including edge effects under current (a1) and a projected future road network scenario (b1).

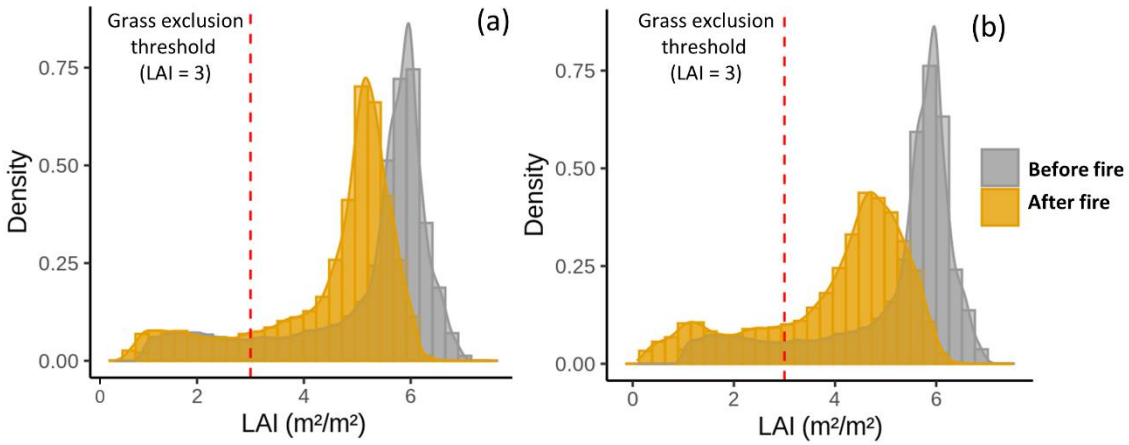

Figure 3 - Density distributions of Leaf Area Index (LAI) before and after a fire for the Amazon region under current (a) and future (b) climate scenarios. Red dashed lines indicate the grass exclusion threshold (LAI = 3), above which the forest has sufficient canopy cover to exclude shade-intolerant grasses.

The risk of a forest shift to an alternative grass-dominated state was considered to be especially high where the FRI is already shorter than the canopy recovery time. There were substantial spatial differences in simulated recovery time as function of climate (post-fire time required to achieve LAI = 3). The southern and southeastern parts of the basin currently require the longest recovery times with mean of 4.6 years and median of 5.1 years. (Figure S5). Mean fire return intervals in the Amazon were lowest in human dominated areas, where FRI ranges from 1 to 10 years (Figure S6). Estimated increases in the frequency of fires as a result of grass invasion would result in a fivefold increase in areas with low fire return interval (from 109,000 to 507,000 km2) as the mean FRI would drop from 5 to 2 approximately (Figure 4).

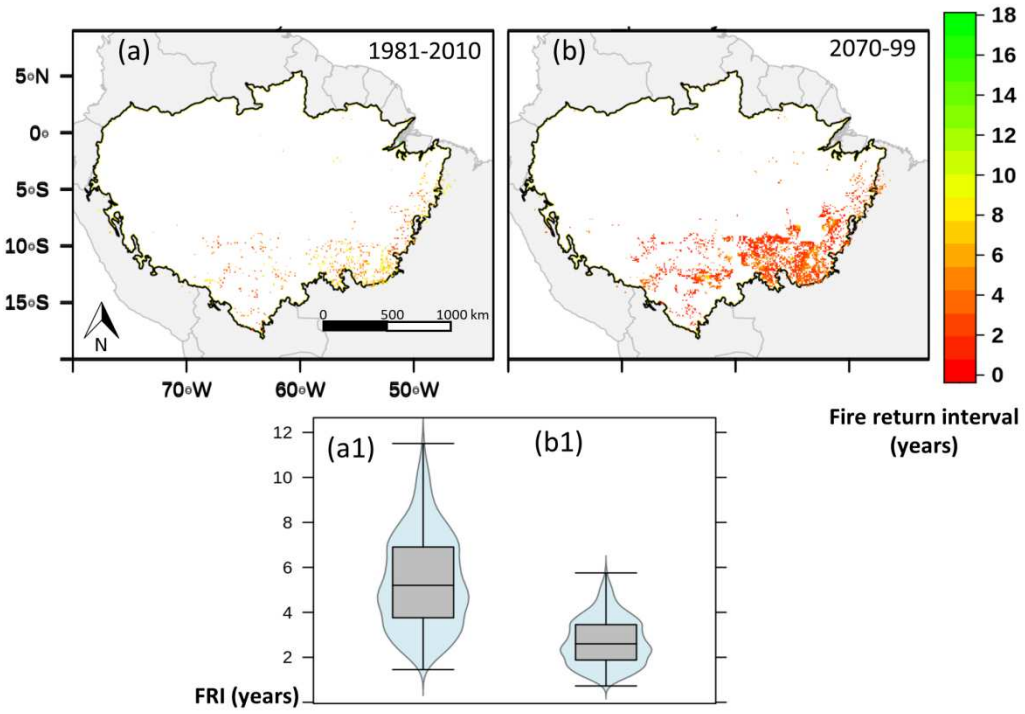

Figure 4 - Fire return interval (FRI), defined as the mean number of years between two successive fire events, within regions with LAI < 3 after fires. For present (a; 2003-2016) and future (b; 2070-99) climates, considering increases in fire frequency due grass-fire feedbacks. The violin plots summarize FRI distributions. The width of each violin is a kernel density function. (a1, b1)

We found that climate change could have substantial impacts on forest resilience in the future. Non-resilient areas, where recovery time exceeds fire return interval, could emerge in approximately 102,092 km^2 under current climate (Fig. 5a), and in about five times this area in the future (562,736 km^2), considering present FRI (Fig. 5b). This implies that approximately 10 % of the forest in the Amazon basin may be at risk of a regime shift to a low tree cover state by the end of the 21st century if burned.

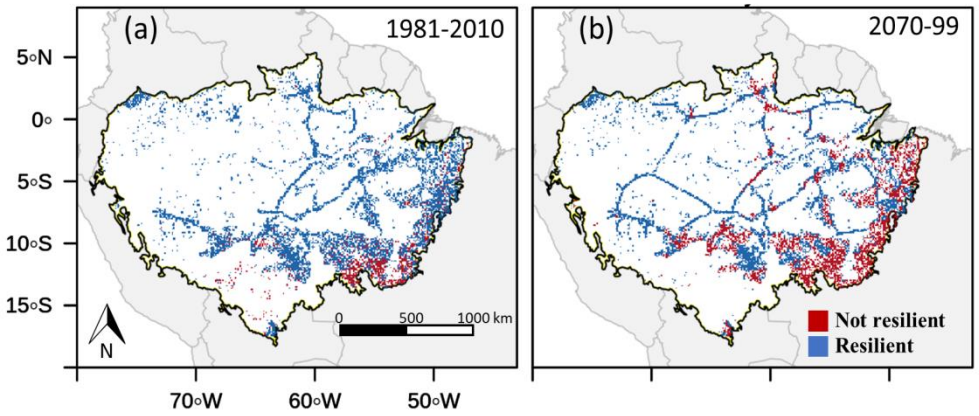

Figure 5 - Resilient and non-resilient forest areas under current (a) and unmitigated climate change (b) conditions. Resilience is based on the difference between Fire Return Interval (FRI) and forest recovery time. A site is considered resilient (blue) when the time required for the forest to recover a LAI of 3 and exclude shade-intolerant grasses is shorter than the FRI, and not resilient (red) otherwise.

3.3 Discussion

We estimated that 6 % of the Amazon is currently vulnerable to grass invasion if a high-intensity fire occurred, and that this percentage would increase to 10 % by the end of the century under unmitigated climate change. The predicted increase in grass invasion vulnerability is mostly due to drier and hotter future climates, promoting higher-intensity forest fires during drought years, causing greater post-fire canopy cover losses. These results suggest that, by creating opportunities for grass-fire feedback to take over the controls of ecosystem dynamics, isolated forest fires can play a key role in triggering shifts between alternative biome states in the future. The direct effect of deforestation is analogous. We found that 9 % of the forest patches in the Amazon were located within 3 km from an edge, most of which was concentrated in the southeastern region.Edge effects resulting from deforestation were predicted to increase the area affected by grass invasion from 338,702 to 809,849 km^2 under present conditions and from 526,358 to 1.15 million km^2 under future conditions, totaling 14 and 21 % of the region respectively. Therefore, even if the Amazon experiences no land cover type conversions until the end of the century, we should expect that isolated drought fire events under climate change coupled

with logging to greatly increase grass invasion in the region, especially in southeastern Amazon.

Currently, fires in the Amazon have mostly anthropogenic origin, resulting from slash-and-burn of forest resources (Nepstad et al. 2001), logging and deforestation (Barlow et al. 2020) as canopy cover usually buffers the vegetation against natural fires generated by lightning (Newberry et al. 2020). Accordingly, our results suggest that fire is higher under more intensified land use. By reducing canopy cover beyond a LAI of 3 in areas near roads, not only grasses would be likely to invade, qualitatively changing fuel type towards more flammable ones, but also forest understory conditions would become drier (Hoffmann et al. 2012). Both factors would greatly increase ecosystem flammability. As a result, these areas could transit from human-driven canopy fires to endogenous grass-fueled surface fire regimes, characterized by a much higher frequency and intensity. For instance, in savanna-dominated landscapes with climate similar to those observed in drier Amazon areas (e.g., Silverio et al. 2013), fire-frequency in forest patches can be ten times lower than in neighboring grassy vegetation under the same climate (Dantas et al. 2013). A similar difference could be expected for forest-dominated landscapes. In fact, the higher (natural) fire frequency observed during the wet, rather than dry season in these isolated and moist savanna-forest landscapes suggest that long dry periods are not necessary for grass curing and endogenous high frequency fire regimes to develop (França et al. 2007; Dantas et al. 2013).

Many locations with high vulnerability to grass invasion already experience recurrent fires. This includes areas that we predicted to require the longest recovery periods, often longer than 5 years. This results in an even higher probability that a subsequent grass-fueled fire would occur before grass exclusion, driving even larger decreases in LAI and/or preventing recovery (Hoffmann et al. 2012, Silvério et al. 2013, Dantas et al. 2016). If fire frequency is not reduced in these areas, the chance that endogenous fire would develop if a catastrophic fire occurs is enormous. These highly vulnerable areas would occupy at least 10 % of the Amazon under unmitigated climate change, approximately 562,000 km^2 (562 million hectares). Thus, in addition to climate change mitigation, intensive fire inhibition policies, especially in more vulnerable areas, could help to prevent irreversible shifts to grass-dominated biome states.

Under both current and future climates, the areas with a high probability of post-fire grass invasion were shown to be concentrated in the southeastern Amazon. This is consistent with previous empirical studies showing that grass invasion after fire already affects some of them (Veldman et al. 2009, Balch et al. 2015). These areas are among those that currently face the highest deforestation rates (Walker et al. 2020). A recent study suggested that this region produces much of the rain supply of western and northern Amazon forests through evapotranspiration (Staal et al. 2018). As a result, canopy cover losses and grass invasion in the southeastern region could greatly increase the frequency of drought events and, thus, the frequency of forest fires, in western and northern areas. This is especially alarming as studies suggest that a reduction in Amazon tree cover levels of 40% could represent the crossing of a regional scale tipping-point with cascading effects for central, southern and eastern Amazon (Lovejoy and Nobre 2018). In fact, while our study did not include Amazonian wetlands, these areas are also considered to be very vulnerable to state shift (Flores et al. 2017).

An important strength of our modelling approach is the fact that model parameters have been specifically calibrated and validated based on data from upland Amazon forests, including the most important fire experiment in the region. Thus, we avoid potential biases related to extrapolating from pattern and processes from other vegetation types and continents (e.g., Scheiter et al. 2013). This is especially important because the plant functional traits that regulate these processes strongly differ among and within (among continents) biomes (e.g., see Dantas and Pausas 2013; 2020). Moreover, our approach combined modelled and observed data, as well as mechanistic and holistic approaches, in order to reduce the uncertainties related to modelling many interrelated variables, which also makes it robust and very simple, that is, parsimonious. Our model also includes the effects of drought on forest structure, fuel loads and drying, a key element modulating the effects of forest fires (Cochrane et al 1999, Nepstad et al 2001, Balch et al. 2008, Brando et al. 2012, Meir et al. 2009). This process is not modelled by most dynamic global vegetation models (Trumbore et al 2015, Powell et al 2013). Finally, our approach explicitly incorporates dispersal limitation of grasses, a process that is often ignored when studying vegetation dynamics (e.g., Scheiter et al. 2013).

At the same time, since all models are wrong by definition and because it is difficult to incorporate all potential influencing local factors when working at this scale, there are some aspects that need to be kept in mind when interpreting these results. For instance, it assumes that the fire impacts in the vegetation are a function of fire intensity alone, as influenced by climatic variability. Yet, fire impacts are influenced by plant traits, such as bark thickness, which can vary in space and time across the Amazon (Staver et al. 2019). Therefore, we assumed that plant communities across the Amazon had similar bark thickness to that observed in our reference site in Southern Amazon (i.e., where the fire experiments were carried; Silvério et al. 2013). In figure 6a we show, using data from Staver et al. (2019), that relative bark thickness (proportion of bark in relation to stem diameter) in the Amazon increases with fire intensity up to a threshold of 149 kW m^{-1}, and then remains relatively stable around the value observed for our reference site (i.e., where the fire experiments were carried; 0.60 $mm.mm^{-1}$; Fig 6). We, thus, report in Fig. 6b the difference in the relative bark thickness of each pixel and that of our reference site (limited to areas within 30 km from a road, where grasses are assumed to be able to invade) and with fire intensity smaller than that threshold (range in which bark thickness increases with fire intensity). These results aim at providing an overall idea of the location, magnitude and direction of potential biases in the estimations of grass invasion probability in our study.

We also assume that the LAI values in the upper stratum (i.e., as captured by our remote sensing products) is representative of those in the ground, that is, that the dynamics of the regeneration stratum (i.e., whether trees resprout or not) is of little relevance at this scale. In support of this assumption, we compiled field data from (Veenendaal et al. 2015; in their Figure 3a) showing that the LAI of the total woody stratum (lower, medium and upper forest strata) at the stand level is very strongly related to that of the upper stratum (see Fig. S2). This is likely to be especially true in the context of this study, which simulates mid to severe disturbances, for which post-disturbance regeneration is fairly well predicted by the CARLUC-Fire model, despite of not considering resprouting explicitly (Hirsch et al. 2004). Our modelling also does not incorporate local factors such as soil fertility or management history. However, as for the variation in soil fertility, a very recent study suggest that soil fertility has little effect in tree-tree competition and plant growth across the Amazon (Rozendaal et al. 2020). Management history, in contrast, is likely to influence forest recovery rates by influencing the proportion of early vs.

late successional forest tree species (Hérault & Piponiot 2018; Elias et al. 2020). There are also several geophysical feedbacks between fire and the environment that could affect the vegetation ability to recover and that are not considered here (e.g., reduction of rainfall; Archibald et al. 2018; Pellegrini et al. 2018; Flores et al. 2019). While these aspects are weakness of our approach, one must consider that efforts to accurately predict spatial varability in forest succession in the Amazon are on very early stages (e.g. see Norden et al. 2015).

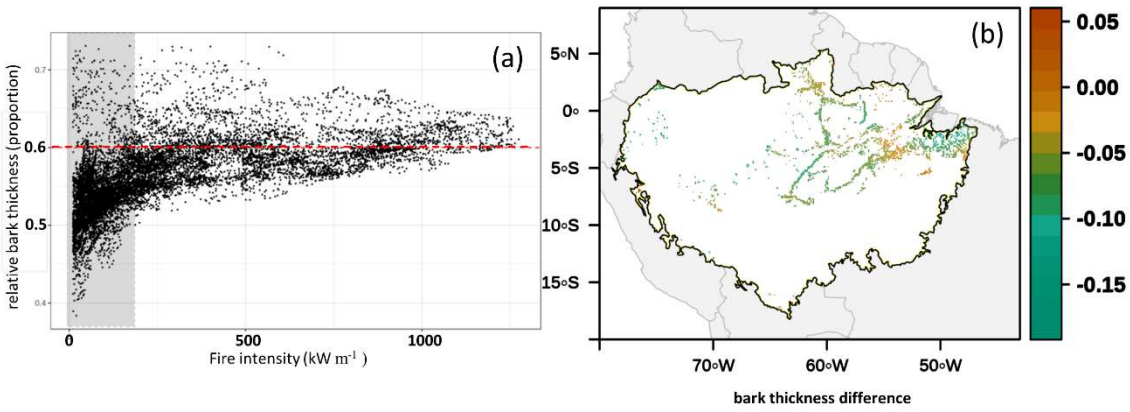

Figure 6 - Uncertainties in the simulated fire effects: Relative bark thickness (proportion of stem diameter) in the Amazon in relation to fire intensity (a) and the values observed in our reference fire experiment site (b). (a) relationship between relative bark thickness (from Staver et al. 2019) and fire intensity (from CARLUC-Fire) for 30,000 randomly selected points across the Amazon. The shaded rectangle indicates fire intensities at which bark thickness increases with fire intensity (breakpoint detected to be 149 kW m^{-1} using a supF test; $P < 0.001$). (b) relative bark thickness differences between the pixel mean value and that of the site for which CARLUC-Fire was calibrated (i.e. Silvério et al. 2013) for areas with fire intensity of less than 149 kW m^{-1} that fall within 30 km from a road (where grasses can disperse). In (b), positive values indicate areas in which grass invasion may have been over- (and negative areas in which it could have been under-) estimated, due to higher (lower) bark thickness in relation to the reference site.

3.4 Conclusion

In this study, we have shown that large parts of the southern and southeastern Amazon, as well as scattered areas in other zones, are at risk of post-fire grass invasion. Some of these areas may already experience sufficiently frequent fires to cause a shift to a grass-dominated state, and these areas could dramatically increase in response to climate change and fragmentation. Although resilience in canopy regeneration is evident in areas with low fire frequency, increased fire frequency due to climate change, deforestation and fragmentation, as well as the associated feedbacks, including grass invasion, could preclude the regeneration of forest cover and push these ecosystems towards a tipping point. If such a transition occurred in large areas it would have major impacts for Amazonian biodiversity (Barlow and Peres, 2008), as well as on the ecosystem services provided by the forest at both local and global scales. To avoid these negative impacts, two complementary strategies could be required. First, global action to limit greenhouse gas emissions is required in order to prevent severe climate change. Second, in order to limit anthropogenic fires, we recommend the creation of new protected areas, the implementation of effective monitoring systems, and that fire-free agricultural practices that do not use exotic grasses are encouraged, especially in the most vulnerable, southeastern, part of the basin.

DATA AVAILABILITY STATEMENT

This study is based exclusively on open data from open sources. R code for climate analysis can be obtained upon request from the author.

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SUPPORTING INFORMATION

Equation S1: Relationship between MCWD and changes in biomass (Phillips et al 2009)

$$\Delta AGB = 0.3778 - 0.052 * \Delta MCWD \text{(Eq. S1)}$$

where ABG represents predicted losses in ABG and MCWD the maximum climatological water deficit.

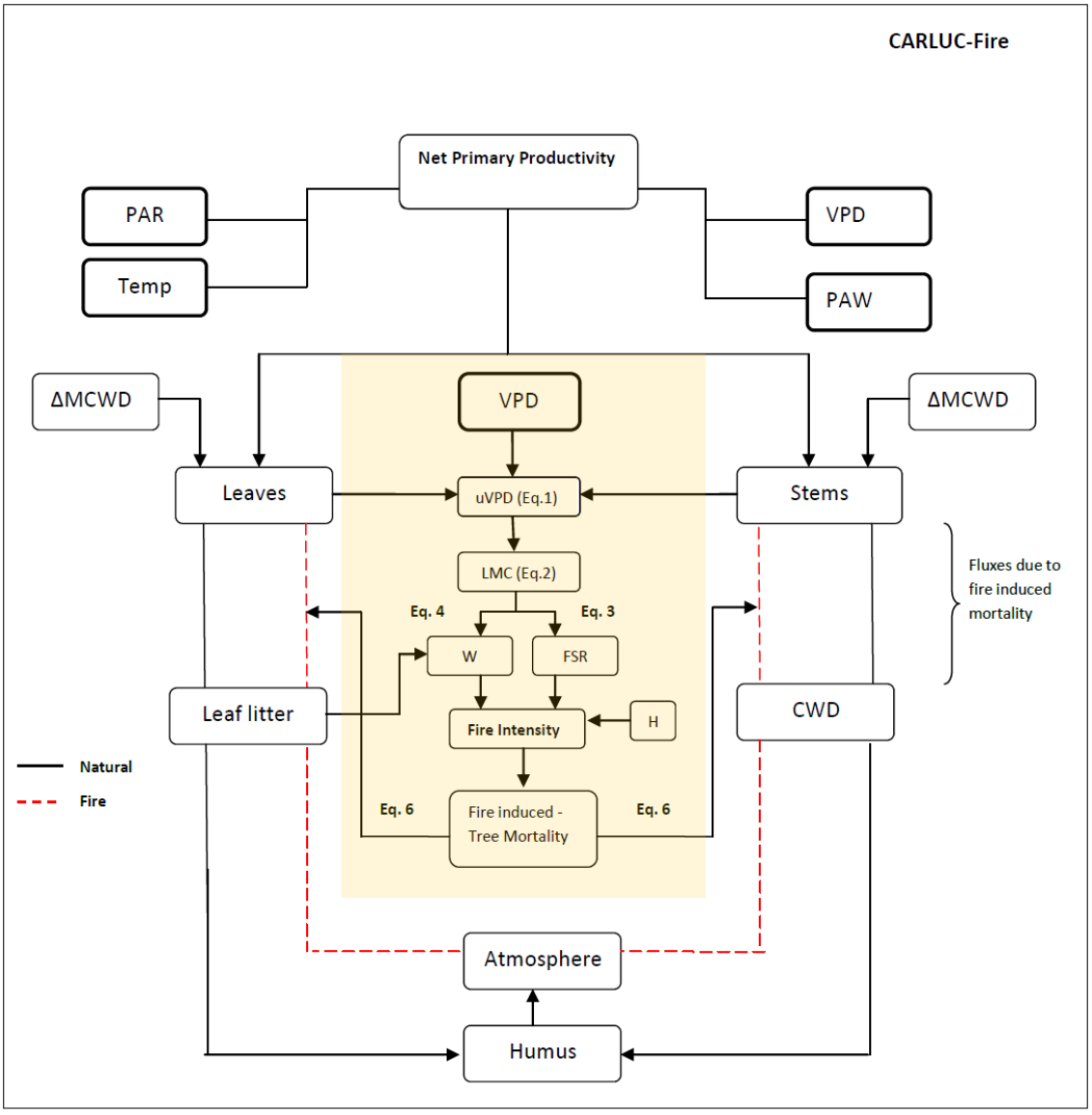

Figure S1 - Flowchart of the model focused in this study, in light orange the fire component

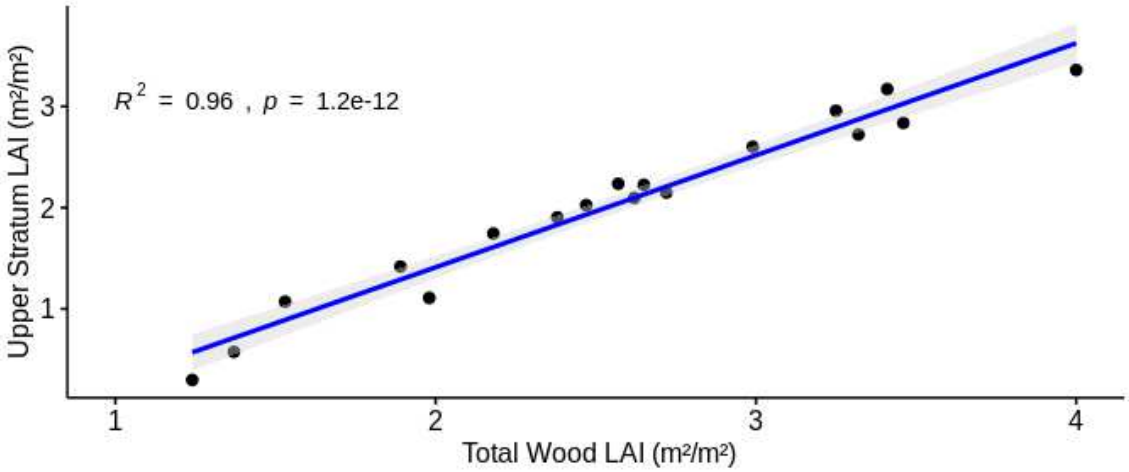

Figure S2 Relationship between the upper woody stratum LAI and the total LAI of woody species in the field for tropical forests (data from Veenendaal et al. 2015).

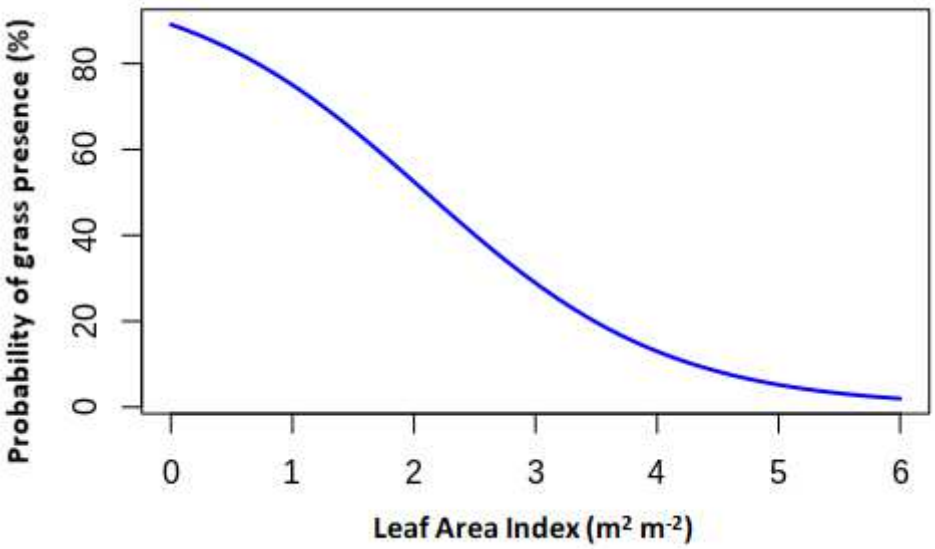

Figure S3- Probability of grass presence as a function of LAI from field measurements (R^2 = 0.6) (Silvério et al. 2013; Eq. S2)

Equation S2: Probability of grass presence as a function of LAI

Prob. grass invasion = $100 * \frac{(1-\exp(\mathrm{LAI}-2.09))}{(1+\exp(\mathrm{LAI}-2.09))}$ **(Eq. S2)**

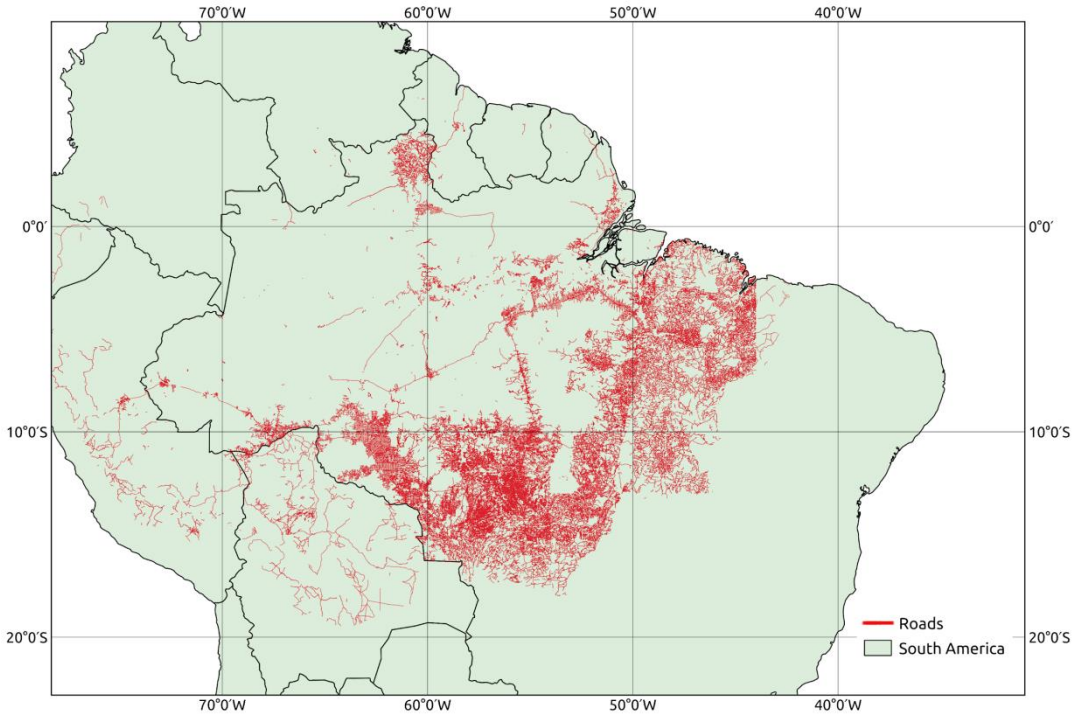

Figure S4 - Paved and dirt roads throughout the Amazonia (Soares-Filho et al. 2006)

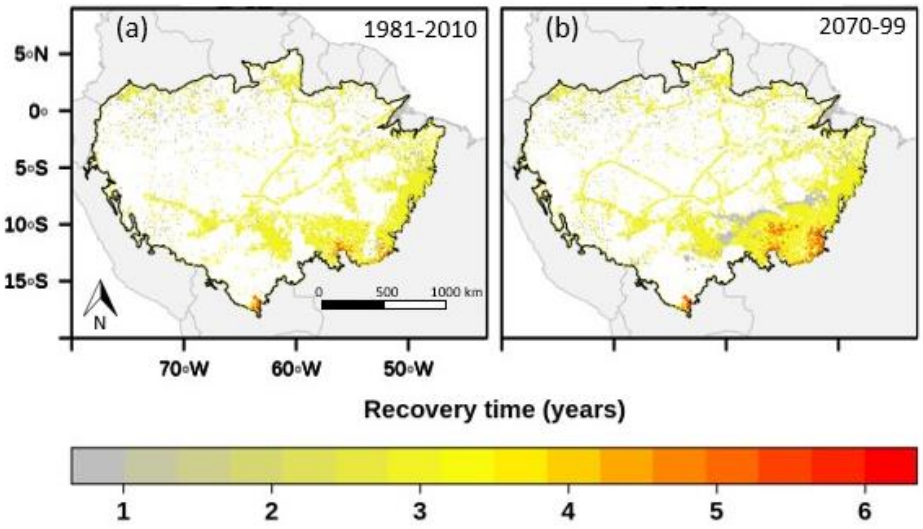

Figure S5- Present (A) and future (B) recovery time required for grass exclusion in the Amazon region. Grass exclusion occurs when the forest develops a critical amount of canopy cover (Leaf Area Index = 3) at which shade-intolerant grasses are outcompeted by forest trees.

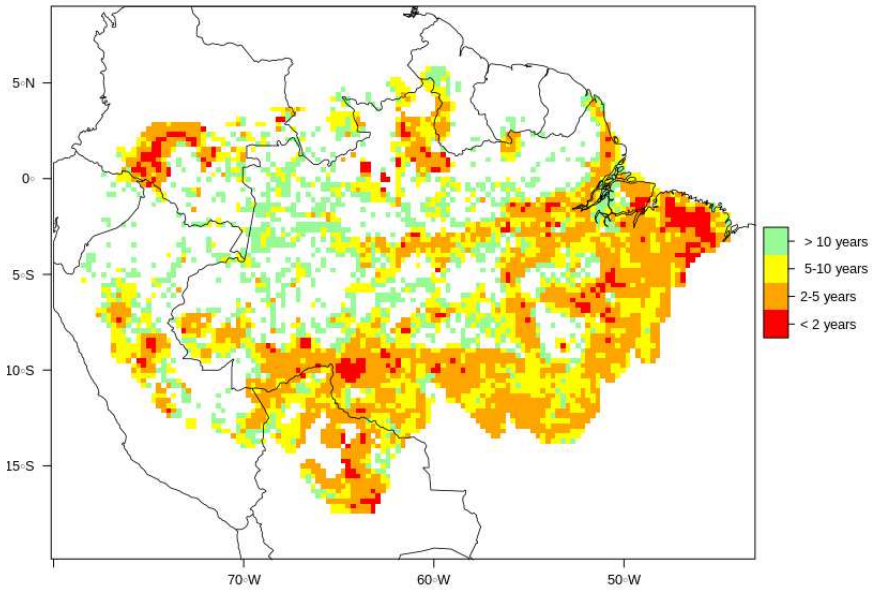

Figure S6 - Mean fire return interval during 2003–2016 at 0.25° gridded.

Table S1: Principal equations of fire behaviour model (CARLUC-Fire)

Variable	Name	Unit	Equation	Eq. #
uVPD	Inner Vapor Pressure Deficit	Kpa	$\text{uVPD} = 0.140494 - 0.006 * Cstem * 10 - 0.594074 * \sqrt{(Cleaf * 10 + 0.5)} + 1.505 * \sqrt{(VPD + 0.5)}$	1
LMC	Litter Moisture Content	%	80 * exp(-0.9 * uVPD)	2
FSR	Rate of Spread	m/min	0.043 + 0.83 * exp(-0.107 * LMC)	3
W	Mass of fuel consumed by fire	Kg/m²	$W = \begin{cases} 1.0, \frac{LMC}{me} < 0.18 \\ 1.2 - 0.62 * \frac{LMC}{me}, \ 0.18 \leq \frac{LMC}{me} \leq 0.73 \\ 2.45 - 2.45 \ \frac{LMC}{me}, \ \frac{LMC}{me} > 0.73 \end{cases}$	4
FI	Fire Intensity	kW/m	$W * FSR * H$[a]	5
Mort	Mortality[b]	Kg/m²	$\frac{1}{1 + exp(2.45 - 0.002373 * FI)}$	6

Cstem: Carbon in stems. Cleaf: Carbon in leaves.Cllstruc: Carbon in structural leaf litter. Unit for all carbon pools (kg/m²)

[a] *The combustion heat (H), which is assumed to be constant at 18 700 kJ kg⁻¹ (Van Wagner 1973, Albini 1976); and mass of fuel consumed by fire (W), which is based on the assumption that the proportion of each dead fuel class that is consumed by fire decreases as a function of its moisture content relative to its moisture of extinction (me; following Peterson and Ryan 1986).*

[b] *fire-induced tree mortality (i.e. biomass turnover).*

Table S2: Parameters description and their values used in CARLUC Model (modified from Hirsch et al., 2004)

Parameter	Description	Mean value ± error term
Y	NPP/GPP ratio (i.e., CUE)	0.47 ± 0.05(dimensionless)
α	Canopy quantum efficiency	0.035 ± 0.005 (mol C mol uAPAR^{-1})

SLA	Specific leaf area	20 ± 5(m^2 kg leaf C^{-1})
P_w	Fractional allocation to wood	0.4 ± 0.04(dimensionless)
P_f	Fractional allocation to foliage	0.25 ± 0.025 (dimensionless)
P_r	Fractional allocation to fine roots	0.35 ± 0.035 (dimensionless)
F_h	Fraction of decomposed dead organic matter passing to humus	0.17 ± 0.017 (dimensionless)
F_m	Metabolic/structural ratio in leaves and roots	0.1 ± 0.01 (dimensionless)
PAR	Incident photosynthetically active radiation	Model input (MJ m^{-2} $month^{-1}$)
λ	Fractional absorption of PAR by foliage	0.7 (per unit LAI)
τ_w	Turnover time of live wood	600 ± 60 (month)
τ_f	Turnover time of live leaves	12 ± 6 (months)
τ_r	Turnover time of live roots	12 ± 6(months)
τ_m	Turnover time of the metabolic fraction of leaf and root litter	4 ± 0.4 (months)
τ_s	Turnover time of the structural fraction of leaf and root litter	48 ± 4.8 (months)
τ_h	Turnover time of soil humus carbon	300 ± 30 (months)
τ_{wd}	Turnover time of woody debris	60 ± 6 (months)
τ_{wp}	Turnover time of wood products	120 (months)

4 CHAPTER 3 - MODEL-BASED ESTIMATION OF AMAZONIAN FORESTS RECOVERY TIME AFTER DROUGHT AND FIRE EVENTS

Abstract: In recent decades, droughts, deforestation and wildfires have become recurring phenomena that have heavily affected both human activities and natural ecosystems in Amazonia. The time needed for an ecosystem to recover from carbon losses is a crucial metric to evaluate disturbance impacts on forests. However, little is known about the impacts of these disturbances, alone and synergistically, on forest recovery time and the resulting spatiotemporal patterns at the regional scale. In this study, we combined the 3-PG forest growth model, remote sensing and field derived equations, to map the Amazonia-wide (3 km of spatial resolution) impact and recovery time of aboveground biomass (AGB) after drought, fire and a combination of logging and fire. Our results indicate that AGB decreases by 4%, 19% and 46% in forests affected by drought, fire and logging + fire, respectively, with an average AGB recovery time of 27 years for drought, 44 years for burned and 63 years for logged + burned areas and with maximum values reaching 184 years in areas of high fire intensity. Our findings provide two major insights in the spatial and temporal patterns of drought and wildfire in the Amazon: (1) the recovery time of the forests takes longer in the southeastern part of the basin, and, (2) as droughts and wildfires become more frequent—since the intervals between the disturbances are getting shorter than the rate of forest regeneration—the long-lasting damage they cause potentially results in a permanent and increasing carbon losses from these fragile ecosystems.

4.1 Introduction

Natural disturbances have a key role in forest ecosystem dynamics [1], yet global changes in climate and land-uses have intensified disturbances rates in several biomes with important consequences on the ecosystems resilience [2]. Events like droughts and wildfires are becoming widespread phenomena in vast areas of the globe, potentially affecting the ecosystem services they provide [3,4] even in humid biomes with high rainfall rates, such as Amazonia [5–7]. Housing more than half of the world's remaining rainforest areas, Amazonian forests account for considerable carbon storage in living biomass and soils, estimated at around 150–200 Pg [8,9]. In addition, the region represents one of the most important biodiversity hotspots of the planet [10,11]. Amazonian forests are under considerable pressure due to the increased

frequency and intensity of disturbances in moist tropical regions [12]. Forest fires and large-scale drought events are both directly dependent on climate [13] and their effects are expected to become more severe with climate change effects (i.e., mostly warming and reduction in precipitation). In combination with human activities, such as selective logging and other land-use changes, increasing fire and drought severity are expected to cause significant forest losses [14].

The Amazon Basin's historical baseline of disturbances has been heavily altered in the last 20 years as a result of anthropogenic activities, increasing the rates of deforestation, drought and wildfire and their impacts [15]. In the early 2000s, logging activities affected ca. 10,000–20,000 km^2 $year^{-1}$ of tropical forests in the Brazilian Amazon and it is estimated that understory fires destroyed ca. 85,000 km^2 of standing forests in the period 1999–2010 [16,17]. Moreover, recent studies have shown that Amazonian forests are becoming more exposed to droughts [18,19], including extreme drought events that would not be expected to take place more than once in a century (e.g., the three devastating droughts of 2005, 2010 and 2016; [20,21]). Altogether, droughts, wildfires and logging activities increase the susceptibility of forests to successive burning by increasing ignition rates, wind speed, creating drier microclimatic conditions near the soil surface and promoting exotic grass invasion. The effect of fire in forest ecosystems contrasts with that observed at larger spatial scales (i.e., global scale) and in fire-prone regions in which anthropogenic influences often reduce fire spread [22]. Therefore, the increasing risk of wildfires is an additional driver of change in the Amazon region [23].

Forest degradation due to more frequent and intense disturbances in the Amazon [24,25] results in long-term reduction in carbon stocks [26] with potential release of the C stored in Amazonian forests. The degree of degradation of the forest C stocks depends on four major factors: (1) the type of disturbance (e.g., logging, droughts and wildfires); (2) intensity (i.e., percentage of C loss); (3) the time return interval (i.e., years from one event to the next one) [25,27,28]; and (4) disturbance synergisms (i.e., the interacting effects between disturbances).

Several studies have analyzed forest recovery after disturbances at either broad or at multiple scales disturbances [29,30], but few of them have been conducted in tropical forests and specifically in the Amazon Basin. When conducted, these studies are usually limited in temporal scale (usually <20 years) [25,31,32] and focus on the effects of a single disturbance and in relatively small areas [33–35]. There is a lack of studies looking at recovery beyond 30–40 years. As a result, we still have a limited understanding on forest aboveground biomass (AGB) resilience to disturbance in Amazonian forests (i.e., how much time does it take for the forest

to return to its pre-disturbance status), especially at the regional scale and taking interacting effects of multiple disturbance into consideration.

One straightforward way of addressing the consequences of disturbance in forest AGB is by integrating geospatial techniques with remote sensing and process-based forest growth models [36,37]. Specifically, remote sensing and GIS technologies allow the assessment of forest AGB at broad scales [38] whereas process-based forest growth models can provide insights on the mechanisms and processes involved in forest recovery and their relationship with spatiotemporal climate (including human)-induced scenarios. Models can help in assessing the recovery time of vegetation using climatic variables to predict vegetation productivity and its spatial variability [38]. At a regional scale, net primary productivity (NPP) is often used as an indicator of inherent plant growth potential [39]. Several studies have indeed assumed a strong relationship between productivity and biomass [40] with the first one being a function of the second. Indeed, the targeted parameter AGB is also influenced by climate, water availability and soil fertility [39–41]. In this study, we assessed the recovery time (i.e., the time necessary for a forest to recover its pre-disturbance AGB levels) of Brazilian Amazon forests AGB from drought, fire and a combination of logging and fire disturbances, using a dynamic forest carbon model that simulates vegetation recovery time as a function of climate scenarios and geospatial data. With the present study, we aim to investigate the recovery time of AGB in the Amazon forests when subject to a disturbance caused by: (1) an extreme drought, (2) a catastrophic fire and (3) a combination of logging and fire disturbances by integrating the existing knowledge [24,42–44] within our modeling framework.

4.2 Materials and Methods

We used a spatially implicit forest productivity model based on the net primary productivity of the 3-PG model (Figure 1) (see *2.1 The Model* section) to estimate forest recovery time (here defined as the time necessary for a forest to recover at its pre-disturbance AGB levels). Analysis of AGB recovery was carried out for the Brazilian Amazon biome, which encompasses about 3.5 million km^2 located between 15° S–5° N and 40° W–80° W. The region consists of one of the largest preserved forests in the world that has been experiencing strong human disturbances in recent times, especially in “the arch of deforestation” (Figure 2).

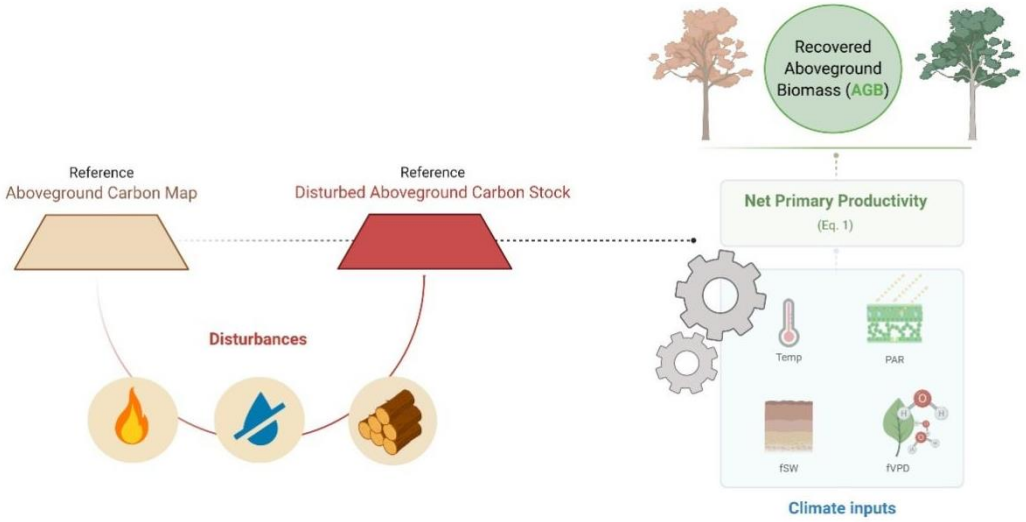

Figure 1. Proof–of–concept vegetation recovery time simulations as a function of climate variables (i.e., soil-plant available water (*fSW*), photosynthetically active radiation (PAR), vapor pressure deficit (*fVPD*), and air temperature (*fTemp*), see *The Model* for description). Aboveground biomass (AGB) losses resulting from drought stress and fire are a function of the maximum climatological water deficit (MCWD, see *The Model* for description).

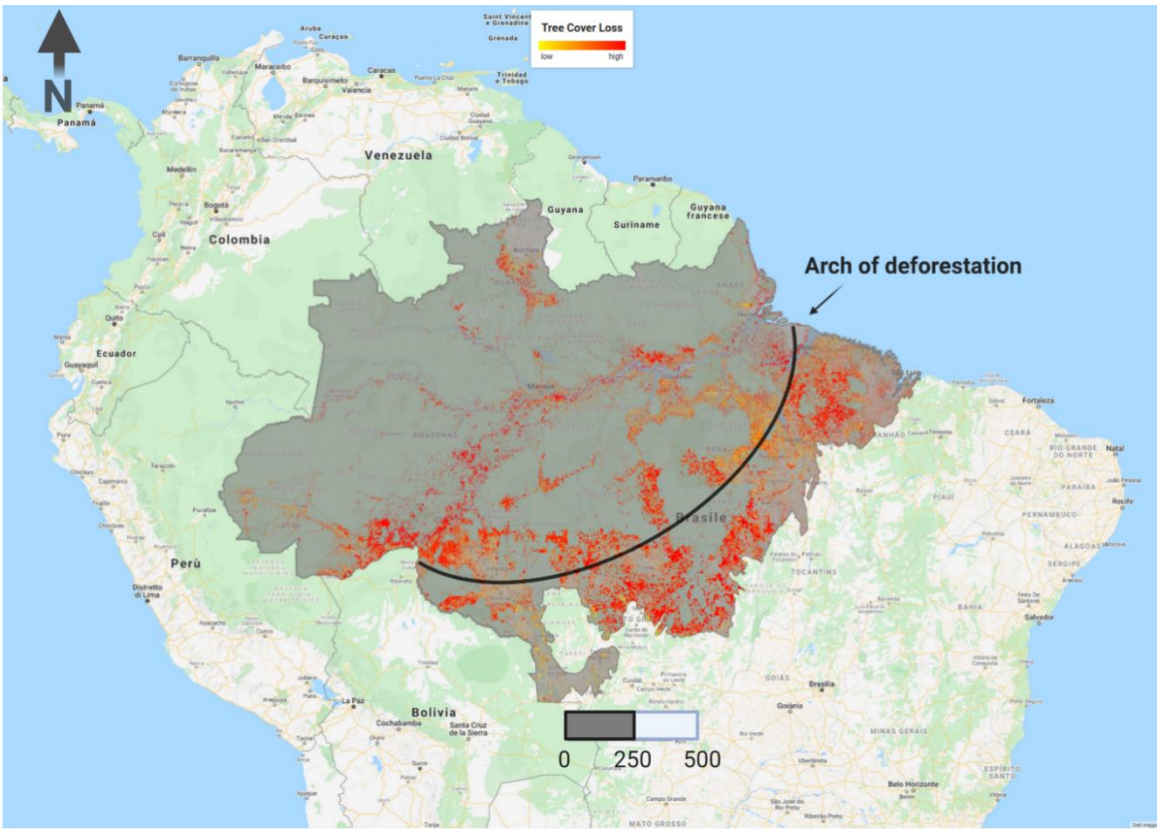

Figure 2. Study area: Amazonian Forest in Brazil. Amazon biome extent (gray area). Forest loss map (yellow-red) has been displayed according to [45,46] (Global Forest Change dataset in Google Earth Engine). Red pixels identify areas of where tree cover loss has been detected.

4.2.1 The Model

In this study, recovery time dynamics are simulated using the 3-PG model (Physiological Principles in Predicting Growth; [47]), as embedded and parameterized into the CARLUG model by [48], driven by four monthly climatic variables: photosynthetically active radiation (PAR, mol PAR m^{-2} $month^{-1}$), vapor pressure deficit (VPD, KPa), precipitation (mm $month^{-1}$) and air temperature (°C), respectively. The 3-PG model was used to estimate gross and net primary productivity (GPP and NPP, both in g C m^{-2} $month^{-1}$) as follows:

$$NPP = GPP \times Y \quad (1)$$

where Y is the carbon use efficiency (i.e., the fraction of GPP not used to support autotrophic respiration, known as CUE [49–51]). GPP is computed as:

$$GPP = \alpha_x \times modifiers \times PAR \times (1 - e^{-k \times LAI}) \quad (2)$$

where α_x is the maximum quantum canopy efficiency (i.e., the maximum capacity in converting light into photosynthates without environmental or other functional limitations, in mol C mol PAR^{-1} m^{-2} $month^{-1}$), *modifiers* comprise environmental limitations to maximum photosynthetic rate (temperature, *fTEMP*; soil water, *fSW*; and vapor pressure deficit, *fVPD*), with values ranging from zero (complete limitation) to one (no limitation). For an in-depth description of modifiers algorithms see also [48,52]. The last two terms in Equation (2) reflect the incident PAR effectively absorbed by the canopies (i.e., APAR) based on their leaf area index (LAI, m^2 m^{-2}) and the leaf light extinction coefficient (*k*, unitless) as in Beer's Law [53].

Each month, the model assumes that leaf, wood, and root carbon pools increase by an overall amount equal to the NPP, which are, respectively, allocated proportionally in their three pools as in the standard 3-PG carbon partitioning-allocation scheme [54]. The partitioning of NPP is the outcome of the climate and soil conditions interacting with vegetation through a series of differential equations that describe the flow of C within the tree compartments [48]. Therefore, the model predicts the distribution of forest biomass from carbon stocks, but in order to obtain biomass we converted C to biomass assuming that one ton of biomass contains 0.5 tons of C [55]. We assume that the re-equilibration of forest carbon after disturbances (i.e., steady state

undisturbed conditions) is when the AGB growth and the decay rates stabilize. We also estimated the average time to recover 90% of old-growth forests' carbon levels. The 90% threshold has often been used in similar studies (e.g., [56]) and can thus more easily be compared to previous results; the 100% threshold corresponds to a full recovery of carbon stocks, but it may take significantly longer.

The study conducted by [48] uses the recalibrated 3-PG model parameters for the Amazonian forests (the overall parameters description and their values are shown in Supporting Information, see Table S1). The 3-PG calculates NPP as a constant fraction of GPP, using an NPP/GPP ratio (Y = 0.47) based on empirical evidence [47]. For Brazilian Amazon forests other studies suggest Y to be closer to 0.3 [57] while others report much higher values at some tropical sites, even including Amazonian ones (i.e., Y > 0.5; [51]). However, the issue of whether Y is a constant value, its actual value, even including its top-down limits, is a much-debated issue as described in [51,58].

An overall 3-PG model parameter sensitivity analysis has been performed already by a number of authors (e.g., [59]) showing how the 3-PG model is mostly sensitive to stem allometric parameters (i.e., those used to obtain from trees structure the tree biomass), ratios for biomass partitioning and allocation, maximum canopy conductance, turnover time of wood, and maximum canopy quantum efficiency. For an in-depth 3-PG model parameter sensitivity analysis we refer to the works of [48,59] and this will be not considered and discussed further here. In addition, we used the pan-tropical biomass map generated by Avitabile et al. [60] as reference (pre-impact) levels to initialize the model and combining it with two comprehensive recent estimates of carbon density (i.e., estimations of [55,61] and covering a wide 250–500 Mg ha^{-1} range (Figure S1).

4.2.2 Estimating Drought, Fire and Logging Impacts on AGB Stocks

The loss of AGB due to drought events was modeled as a function of the MCWD (Maximum Climatological Water Deficit index, representing the maximum climatological water deficit reached in the year), a common index used to measure the cumulative water stress in Amazonia (e.g., [42,62,63]). The MCWD reflects the intensity and length of the dry season, when evapotranspiration exceeds precipitation (i.e., negative balance). A measure of water deficit related to tree mortality in Amazonian forests that is denoted as in Lewis et al. [42], that is:

$$\Delta AGB = 0.378 - 0.052 \times \Delta MCWD \quad (3)$$

we estimated the MCWD anomalies (namely, ΔMCWD) for the year 2010 by first estimating the mean MCWD for the baseline period from 1998 to 2015, without considering both the years 2005 and 2010. The ΔMCWD have been shown to be strong predictors of drought-associated tree mortality in the Amazon [62]. Specifically, a monthly water deficit was calculated as the difference between precipitation and evapotranspiration (with ground measurements estimated at 100 mm per month [63,64], i.e., evapotranspiration is fixed at 100 mm month^{-1}). As a result, we assume that the forest is in water deficit when monthly precipitation falls below 100 mm. MCWD was calculated as the sum of sequential monthly water deficits, where more negative MCWD values indicate higher drought stress. We quantified the MCWD for the year of 2010 using the product 3B43 of TRMM (Tropical Rainfall Measuring Mission at 0.25° grid-resolution), and then, the average of carbon losses for each pixel using Equation (3). The 2010 drought is one of the most intense and spatially extensive drought events ever recorded in the Brazilian Amazon [42].

Effects of wildfire were estimated by using the CARLUC-Fire model [44]. This model specifically accounts for the effects of fire by estimating forest carbon losses after a fire event as a function of its intensity (FI). FI is defined as the energy released per unit length of fire-line (kWm^{-2}), which is a key factor in estimating how vegetation responds to fire events. The relationship between fire intensity and fire-induced biomass losses was derived from a large-scale fire experiment in southeast Amazonia [24,44] (Equation (4)). Based on this experiment, AGB losses were calculated as a function of FI as follows:

$$AGB_{losses} = \frac{1}{(1 + e^{(2.45 - 0.002373 \times FI)})} \quad (4)$$

We limit our fire analysis to areas that burned between 2003 and 2016 [65] using information at 500 m resolution from the Moderate Resolution Imaging Spectroradiometer (MODIS) Collection 6 MCD64A1 burned area product over the period 2003–2016.

As a substantial proportion of fires occurred in areas likely to have been previously logged, we accounted for this effect in the estimation of the initial AGB by incorporating an additional loss in fire effects of 40% in burned areas that were also cleared. We assumed this based on findings of Berenguer et al. [43] that an average forest under selective logging stores about 40% less carbon. Logged areas were defined using data from the annual Landsat-based Project for

Monitoring Amazonian Deforestation (PRODES, http://www.obt.inpe.br/prodes). Because edge effects from logging have been shown to affect forests up to 2–3 km from the border [66], we include forests located within 3 km from a deforested pixel, as a selective logging influence zone and they were defined using data from PRODES with cumulative deforestation up to 2017.

4.2.3 Experimental Runs

We ran the 3-PG model at 3 km × 3 km spatial resolution under mean monthly climate conditions for the 1980–2009 period, to estimate the forest recovery time for both drought, fire and logging + fire impacts (includes loss from logging and losses from fire). Climate input variables used to calculate the climatic means consisted of monthly series of temperature and mean vapor pressure deficit from the Climate Research Unit (CRU TS; [67]), while PAR was obtained from the GOES–9 satellite product [68]. In each pixel, AGB recovery was assessed by simulating AGB dynamics with the model after an AGB loss corresponding to disturbance impact.

4.2.4 Assessing Model Results

Light detection and ranging (Lidar) remote sensing is widely used for monitoring forest structure and biomass dynamics [69,70] in many forest ecosystems [71]. For instance, airborne lidar (ALS) technologies help quantify changes in canopy structure, carbon stocks and recovery time at the local-to-regional scale under different types of forest degradation (e.g., [25,72,73]).

In the present study, we compare our modeled recovery time from fire in logged areas with airborne lidar-derived aboveground carbon density (ACD) recovery estimates in forest stands (2891.45 Ha) located in Feliz Natal (Mato Grosso, Brasil) that were logged and burned once. For computing the recovery time of ACD from lidar, we applied a model developed by Rappaport et al. [25] that used multiple linear regression to model the recovery time of ACD (Kg C m^{-2}) in degraded forest stands based on degradation type. In their study, the model was calibrated using a chronosequence of ACD maps derived from lidar and degradation history data (from 2013 to 2018) across degraded forests stands [20]. The model is presented in Equation (5) and shows adjusted R^2 of 0.89. Herein, we chose to compare our results with those provided in Rappaport et al. [25] due to lack of available field data on the time scale addressed here to assess recovery time.

$$RT = 62.259 + 11.395 \times \log(t) - 10.268 \times CF1$$

where RT refers to recovery time, t refers to time (years) and CF1 refers to degradation history, once-burned stands.

4.2.5 Disturbance Return Interval

In order to inquire whether global changes could determine an increase in future drought and fire frequency we projected the areal extent and spatial patterns of future drought and fire impacts up to the year 2100 in order to understand whether global changes could determine an increase in future drought and fire frequency in the study area. We analyzed both future precipitations (based on Representative Concentration Pathways, i.e., RCP 8.5—representing unmitigated climate change scenario) and a land use changes scenario (based on Aguiar et al. [74]) with a decrease in the extension and level of protection of the areas and increases in deforestation rates from 2014 to 2020 and continuing until 2100.

We built drought scenarios (2040–2070 and 2071–2100) using precipitation (related with water stress, MCWD) from the ensemble of 35 climate models participating in the Coupled Model Intercomparison Project Phase 5 (CMIP-5, [75]). In detail, we derived the forcing from the mean monthly simulated precipitation anomalies first averaged for all 35 models and then bias corrections with Tropical Rainfall Measuring Mission (TRMM data product 3B43 [63]). To investigate frequency of future Amazonian droughts we assumed severe drought condition when MCWD anomalies (subtraction between future projections and the historical average) is <−40 mm (threshold derived by Phillips et al., [62]), below this threshold water stress is assumed to induce losses in AGB. We also used maps of predicted change in fire recurrence in response to global changes obtained from Fonseca et al. [76] based on future land-use change data by Aguiar et al. [74]. The fire scenarios (2040–2070 and 2071–2100) developed by Fonseca et al. [76] combine the effects of future land-use and climate change on fire relative probability in the Brazilian Amazon in the best-case and worst-case scenarios. We assume fire relative probability to equal fire relative frequency and then determine the mean fire return interval as the inverse of fire relative frequency.

3. Results

Results show that disturbances have substantially affected biomass in Brazilian Amazonia. In the locations affected by drought, fire and logging + fire, AGB decreased by 4%, 19% and 46%, respectively (Figure 3). Our results suggest that during the 2010 drought, about 1.5 million km^2 of the Brazilian Amazon lost a considerable amount of AGB (we considered losses ≥10% of

the initial AGB). Fire could also produce substantial losses in above-ground carbon affecting 550,000 km^2 especially in southern Brazilian Amazon. Approximately 150,000 km^2 of the burned forest patches were located within 3 km from a logged forest.

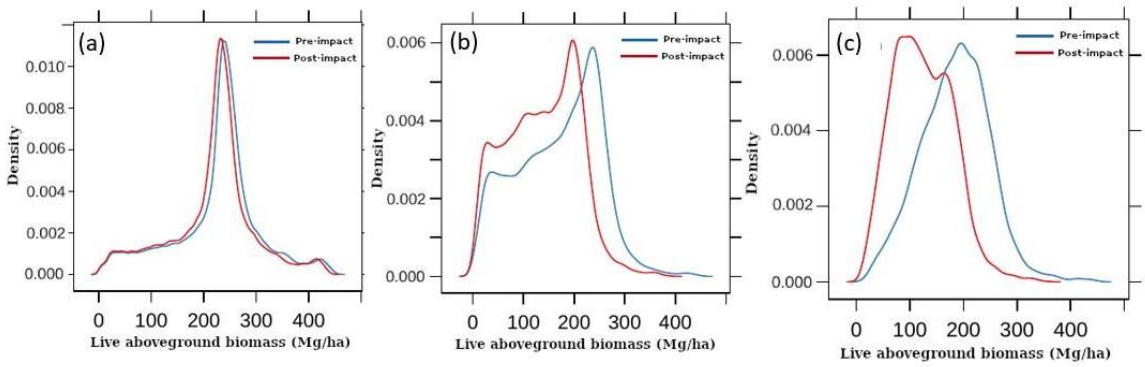

Figure 3. Biomass density plots describing patterns before and after drought (**a**), fire (**b**) and logging + fire (**c**) impacts. Only areas that burned between 2003 and 2016 are considered and, for (**c**), only burned areas up to 3 km from logging areas. Recovery is defined as 100% of pre-disturbance AGB.

Average AGB recovery time was 27 years for drought-impacted, 44 years for burned, and 63 years for logged + burned areas (includes loss from logging and loss from fire). Recovery time from drought revealed a northwest-to-southeast gradient in the study area (Figure 4a). Roughly 20% of these drought-affected areas, corresponding to ca. 364,000 km^2, were estimated to recover in the first 10 years, with maximum values reaching 90 years in parts of southeastern Brazilian Amazonia (Figure 4). Forest fires were widespread across the "arch of deforestation" (the region in southern and eastern Amazonia where the rates of deforestation are higher) during the period 2003–2016 (Figure 4b). The longest recovery times during this period were concentrated along the eastern and southwestern extent of Amazon forests in Brazil, where the maximum was about 150 years after fire disturbance. Subsequent wildfires events (i.e., multiple fires in the same location) accounted for 10% of all forest fires during the period 2003–2016, delaying forest recovery times within these areas (Figure 4b). The longest recovery times were found in logged-and-burned forests with maximum values reaching 184 years (Figure 4c, c1). These results consider a recovery of the carbon stock corresponding to 100% (i.e. recovery time ~184 years) (see *The Model*) resulting in a difference of about 122 years in logged and burned forest which would be much faster if we would consider a recovery threshold of 90% (i.e. recovery time ~62 years) (Figures S2).

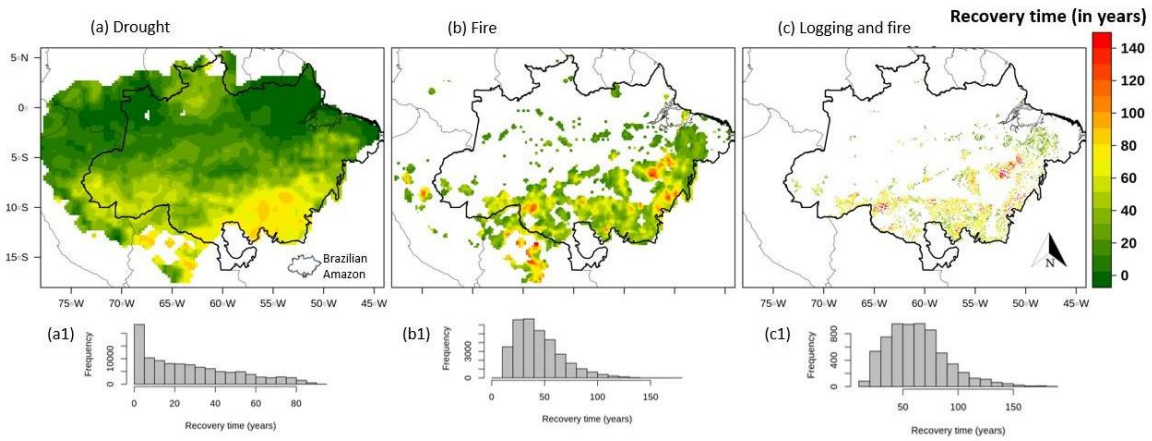

Figure 4. Aboveground recovery time (in years) for 2010 drought (**a**), fire areas that burned between 2003 and 2016 (**b**) and in areas that were both burned and logged (**c**). Histogram plots summarize AGB recovery pixels distributions (in years), for drought (**a1**), fire (**b1**) and logging + fire (**c1**).

We compared our results with a lidar-derived model of recovery time in stands that were logged and burned once (Figure 5a). Our estimations show smaller AGB decreases in comparison with lidar-based estimates of carbon losses from fire (loss of AGB of 46% vs. 55%). However, recovery rates were shown to be strongly correlated (Figure 5b).

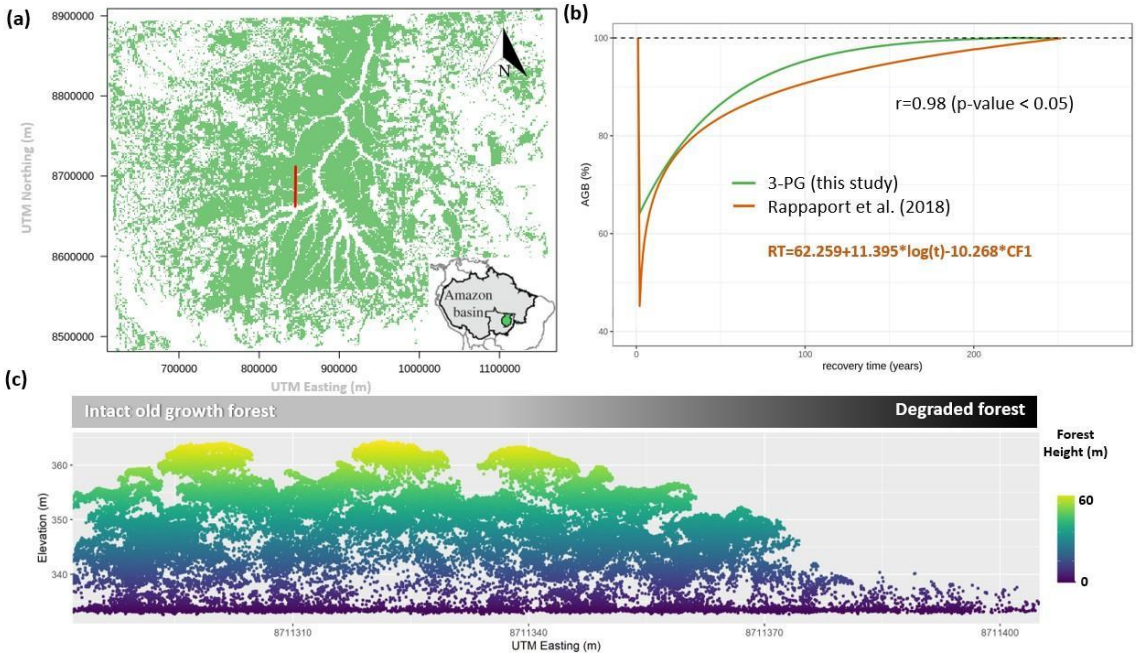

Figure 5. Airborne light detection and ranging (lidar) data were sampled (red line) in Feliz Natal, within the Xingu basin (light green), Brazilian state of Mato Grosso (**a**). The forest growth model (3-PG green line) shows the relationship between aboveground biomass (%) and recovery time in years. We compared it with a lidar-derived model of recovery time in stands that were logged and burned once (CF1 refers to once-burned) [25] (orange line) (**b**). A sample of vertical profile of a recovering forest which was degraded by fire and selective logging (**c**). The discrete return lidar data used for creating the transect figure were acquired in 2018 with a point density of 22.98 points m^{-2} covering an area of 2891.25 ha in Feliz Natal, Mato Grosso, Brazil [25], as part of the Sustainable Landscapes Brazil project program (data available from: https://www.paisagenslidar.cnptia.embrapa.br/webgis/; details of airborne lidar (ALS) data acquisitions are presented in the supplementary material, Table S2).

Increases in the extent and frequency of drought and fire (Figure 6) suggest that these future disturbances could undermine the full forest recovery. Our results suggest that by 2070 the area affected by drought will increase approximately three-fold (Figure 6—top panel). Moreover, from the middle to the end of the century, the mean fire return intervals (FRI) was projected to decrease from 10 to 8 years and the median FRI to decrease from 8 to 6 years from the 2040–2070 period to the 2070–2100 periods, respectively, in a worst case land use change scenario (Figure 6 bottom panel). However, in a more optimistic scenario the area subject to high fire frequency would be smaller (Figure 6 middle panel).

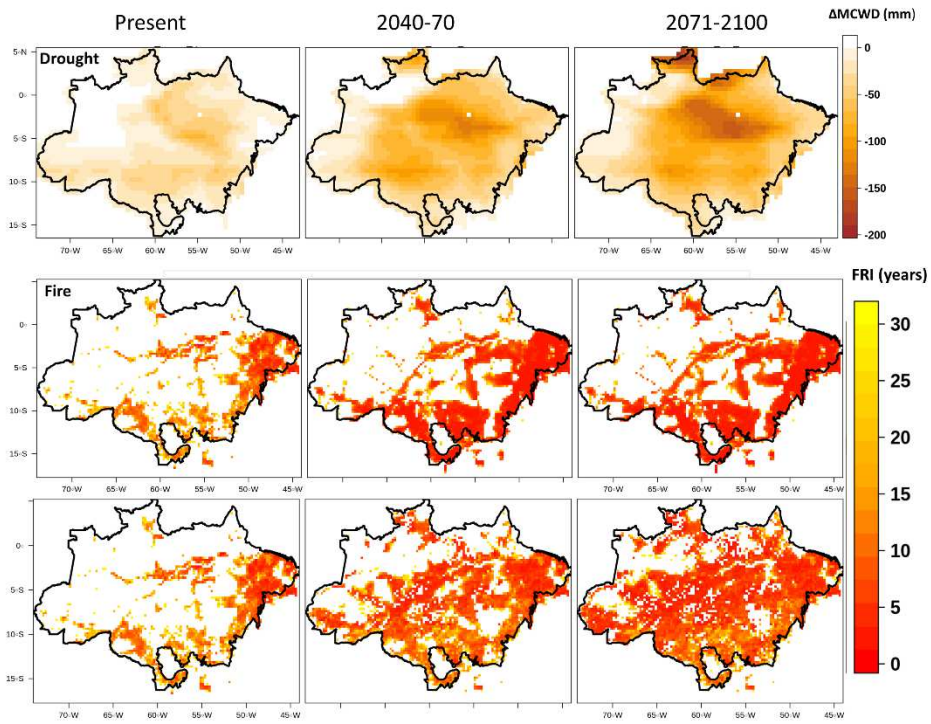

Figure 6. Projected changes in droughts (as maximum climatological water deficit anomalies, ΔMCWD) (upper panel) and fire return interval based on an optimistic land use scenario (mid panel) and in the unmitigated scenarios with the worst-case land-use scenario (bottom panel).

4.2.6 Discussion

In the present study, we explored the AGB changes after drought, fire and a combination of logging and fire disturbances and the time needed for complete recovery as a function of both climatic conditions and AGB in the Brazilian Amazon forest, using a modeling-based approach. Our results suggest that fire is a much greater threat than drought for the forest resilience, especially if logging occurs. These results highlight the key threat imposed by fire to Amazon forests. The intensity of the disturbance event is strongly related to both the amount of AGB lost and the recovery time of the forest. The biomass recovery rates estimates reported here are consistent with those from Poorter et al. [56] that showed AGB of Neotropical second growth forest took a median time of 66 years to recover to 90% of previous growth values after multiple disturbances events, including land use changes. On the other hand, recent evidence [77] suggests that recovery time might take at least 150 years until secondary forests (re)gain carbon

levels similar to primary forests, after drought disturbances thus indicating that these biomes have recovery rates that are much lower than previously suggested.

Our results also suggest that by the end of the century, especially after 2070, the Brazilian Amazon will be affected by more frequent droughts with the southern area being more vulnerable since it will need a longer time to recover after these events. Thus, climate change will greatly increase the threat imposed to the forest, potentially jeopardizing forest resilience. The interplay between longer forest recovery times and more frequent droughts has been previously evidenced in the Amazonia, where longer recovery times have been documented [78]. Moreover, if on the one hand the extreme droughts of 2005, 2010 and 2016 have prevented the full recovery of the forests, on the other, drought effects on forest canopy carbon fixation capacity could potentially persist for several years during recovery processes [78], leading to forest degradation and changes in forest species composition, and evidence suggests that taller tree species have significantly higher mortality than small tree species, when subject to drought [79,80].

Our findings also confirm that the land carbon sink in the Brazilian Amazon will be strongly impacted by a regime of a chronic state of incomplete recovery [78], with adverse consequences also on the GPP due to shifts in precipitation patterns caused by anthropogenic emissions [81–83]. Indeed, across Amazon forests, GPP is modeled to decrease linearly with increasing seasonal water deficit [82]. Longer and more intense dry seasons have been forecasted, together with an increased frequency and severity of drought events [84–86] and future Amazon droughts are expected to become even more frequent [87,88]. Our projections suggest about one extreme drought per decade (drought return interval ranging from 4 to 16 years depending on the scenario of climate change). If drought frequency increases, Amazon forest, both as species composition and regional carbon sink, will be affected, which will thereby have an impact on global carbon cycling and contribute further to climate change [62,80,89,90]. Previous studies have shown increased fire occurrence and tree mortality during and after Amazon droughts [6,89,91–93]. If these events continue to increase in frequency, large parts of the Amazon could potentially shift from rainforest vegetation to a fire-maintained degraded forest and may promote the persistence of degraded forests with a savanna-like structure [94,95]. This change in forest type, structure and ecology would most likely reduce both the forest sink capacity and even its biodiversity and ecosystem services [94]. The net increase in areas that are more susceptible to wildfires, induced by either drought events increase, or potentially intensified by climate change, could lead to significant biomass losses [9,96].

Human pressures play a crucial role in fire ignitions, wildfires could break out also in non-dry years as in 2019, when more than 69,000 km^2 burnt despite the absence of anomalous drought [97]. As droughts and wildfires are expected to become more frequent, the time of occurrence between these disturbances may even get shorter than forest recovery time, determining permanently damaged ecosystems and widespread degradation [95]. Although forest growth models are powerful tools that can be applied in simulating the C dynamics in forests [98,99], our results are subject to some uncertainty and a number of caveats [100,101]. In this study, we modeled vegetation recovery time as a function of climate only. This approach does not account for regional variation in growth rates depending on soils types (due to their inner physico-chemical properties such as water retention or local-scale variation based on prior land use [92,93]) growth rates are also known to vary significantly by species [43]. In addition to the mechanisms mentioned above, CO_2 fertilization of Amazonian vegetation and nitrogen deposition could play an important, but yet often neglected, role in forest regeneration [102]. It has also been suggested that atmospheric CO_2 generally stimulates plant growth with increased rates in photosynthetic activity and indirectly through increased water-use efficiency [103], but not in all cases [104]. As CO_2 accumulates in the atmosphere, Amazonian trees may also accumulate more biomass resulting in denser canopies and faster growth [105]. But an increased atmospheric CO_2 concentration necessarily implies an increase in mean air temperature which is in turn speculated to increase plants' respiration and should result in a levelled-off forest carbon use efficiency [83]. Recent studies indicate that the ability of intact tropical forests to remove carbon from the atmosphere may be already saturating [9,106] while others indicate for tropical species higher thermal acclimation capacities to buffer C–losses by respiration [51], thus, calling for more studies on the possible consequences of warming and increased atmospheric CO_2 concentration on forest dynamics. However, in the Amazon phosphorus is an important limiting nutrient over large parts and its low availability may limit positive CO_2 fertilization effects.

4.2.7 Future Possibilities for Model Improvement

Lidar-derived 3D-point cloud and biomass products can be used to enhance models' representation of complex and heterogeneous forest ecosystems, such as those found in Amazonia [107], and therefore can be used as input or to initialize vegetation models [108]. For instance, Longo et al. [109] have used lidar to obtain initial conditions for an ecosystem model that requires an initial state for forest structure. Their method to derive the vertical structure of the canopy from

high-resolution airborne lidar successfully characterized the diversity of forest structure variability caused by human-induced forest degradation (such as logging and fire).

This new approach has strong implications on modeling recovery time and the successional trajectories of the Amazonian disturbed forest because it does not require any assumption on the successional stage of the forest, but only the vertical distribution of returns. Moreover, it could be adapted to space-borne lidar data, including NASA's Global Ecosystem Dynamics Investigation (GEDI, [110]). Fusion of GEDI and optical data [111] will further expand the spatial extent of available lidar data and potentially provide tools capable of mapping drought, fire and logging impacts helping models to assess recovery time. Moreover, integration of GEDI with either optical or radar [112] wall-to-wall data could allow large-scale characterization of forest ecosystems structure providing accurate measurements of biomass stock that could be used for assessing recovery time via repeated measurements.

4.2.8 Conclusions

This study shows how forest growth models can be used as tools for complementing field-based studies on recovery time by investigating the spatial and temporal dynamics and processes of forest recovery. Indeed, our biomass recovery map illustrates both spatial and climatic variability in carbon sequestration potential due to forest re-growth. By mapping potential for biomass recovery across Amazonia, policy makers could focus their efforts on specific areas that require special protection and need to be preserved. Moreover, such recovery maps could also help by identifying areas with higher carbon sequestration potential thus supporting policies and concrete actions to mitigate forest degradation in areas where biomass resilience is under increasing stress (such as southeastern Amazonia). The capability and timing of forest recovery after drought, fire and logging are urgent and hot topics for applied research calling upon conservation and policy actions in Amazonia. Future changes in fire regimes could push some Amazonian regions into a permanently drier climate regime and weaken the resilience of the region to possible large-scale drought–fire interactions driven by climate change. We are far from an integrated view of forest recovery processes, yet the results presented in this study may provide some new insights about forest recovery time after disturbances. The consequences that an extreme climatic event, such as a drought, may cause in the forest can result in a net loss of ecosystem services compromising these ecosystems dynamics in the long term. As a major result of projected increases in fire and drought frequency and intensity in the region, Amazonian forest resilience appears, in the medium and long term, to be severely jeopardized.

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4.4 Supplementary Material

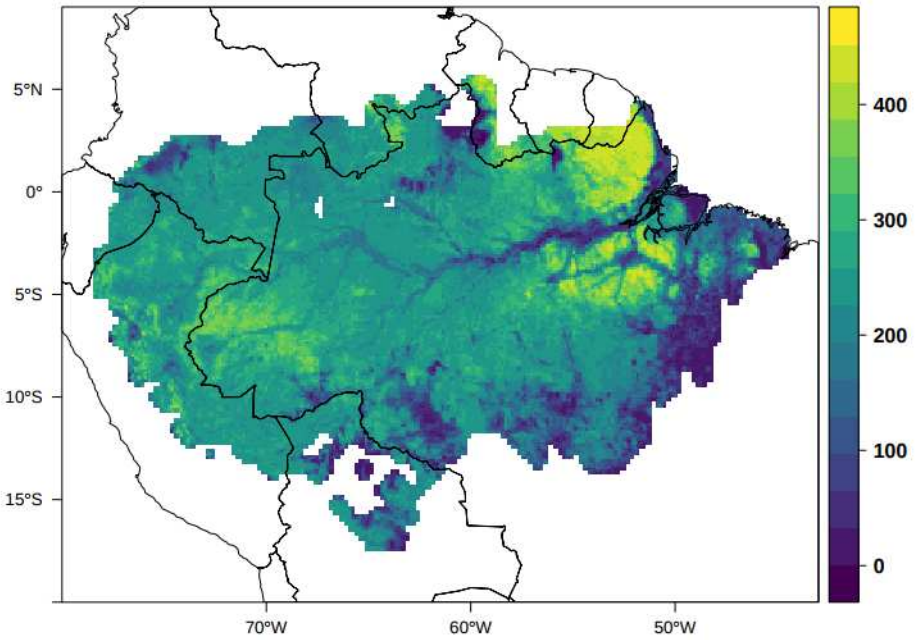

Figure S1. Pre-disturbance reference biomass map [60].

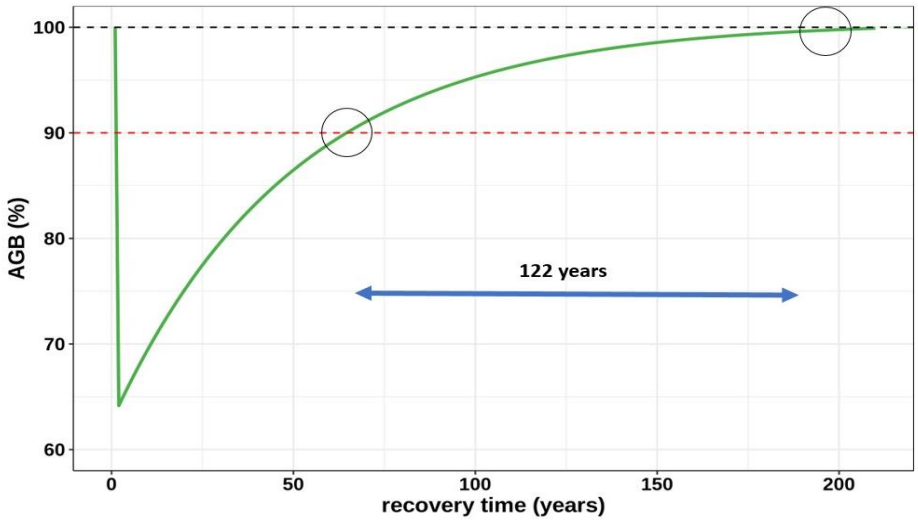

Figure S2. The ABG dynamic as reproduced by the forest growth model (3-PG green line) showing the relationship between aboveground biomass (%) and recovery time in years to reach recovery threshold. Red dotted line 90% threshold and black dotted line 100% threshold.

Tables

Table S1: Parameters description and their values used in 3-PG model (modified from Hirsch et al., 2004)

Parameter	Description	Mean value and units
Y	NPP/GPP ratio (i.e. CUE)	0.47 (dimensionless)
α	Canopy quantum efficiency	0.035 (mol C mol uAPAR^{-1})
SLA	Specific leaf area	20 (m^2 kg leaf C^{-1})
P_w	Fractional allocation to wood	0.4 (dimensionless)
P_f	Fractional allocation to foliage	0.25 (dimensionless)
P_r	Fractional allocation to fine roots	0.35 (dimensionless)
F_h	Fraction of decomposed dead organic matter passing to humus	0.17 (dimensionless)
F_m	Metabolic/structural ratio in leaves and roots	0.1 (dimensionless)
PAR	Incident photosynthetically active radiation	Model input (MJ m^{-2} month^{-1})
λ	Fractional absorption of PAR by foliage	0.7 (per unit LAI)
τ_w	Turnover time of live wood	600 (month^{-1})
τ_f	Turnover time of live leaves	12 (months^{-1})
τ_r	Turnover time of live roots	12 (months^{-1})
τ_m	Turnover time of the metabolic fraction of leaf and root litter	4 (months^{-1})
τ_s	Turnover time of the structural fraction of leaf and root litter	48 (months^{-1})
τ_h	Turnover time of soil humus carbon	300 (months^{-1})
τ_{wd}	Turnover time of woody debris	60 (months^{-1})
τ_{wp}	Turnover time of wood products	120 (months^{-1})

Table S2: Details of ALS data acquisitions

Data Attributes	Value
ALS (Airborne Laser Scanning) system	ALTM 3100
Flight Altitude (m)	750
Acquisition Date	10/05/2018
Scan Angle (º)	10
Scanning Frequency (Hz)	40
Point Density (points/m^2)	22.98
Datum	SIRGAS 2000

5 CONCLUSÕES GERAIS

À medida que as mudanças climáticas se intensificam, alguns ecossistemas podem reagir abruptamente, geralmente com consequências catastróficas para a sociedade (Scheffer et al. 2001). Os efeitos da seca, incêndios florestais, exploração madeireira e efeitos de borda - conhecidos coletivamente como degradação florestal (Hosonuma et al., 2012) podem dominar as perdas de carbono, composição e funcionamento na Amazônia. Isso implica em uma transição crítica onde até mesmo pequenas mudanças na frequência e intensidade de distúrbios poderiam "empurrar" a floresta para um ponto de inflexão, fazendo com que grandes áreas florestais fiquem vulneráveis a transição para um estado de baixa cobertura de árvores mantido por um novo sistema de *feedbacks*.

A importância da floresta Amazônica para a saúde do clima regional e global, já é de conhecimento comum e os resultados discutidos nesta Tese têm implicações importantes em políticas de conservação da floresta. À medida que episódios de seca e incêndio florestais se tornam mais frequentes e intensos, as comunidades florestais podem se tornar mais vulneráveis à mudança para um estado degradado mantido pelo fogo, que favorece a presença de espécies invasoras como as gramíneas. A expansão de áreas invadidas por gramíneas pode, por sua vez, acentuar o risco de degradação permanente da floresta aumentando a inflamabilidade da vegetação sem, no entanto, oferecer condições para a implementação de uma savana com a diversidade vegetal tipicamente encontrada nas regiões antigas de Cerrado. O momento em que o fogo penetra no sub-bosque da floresta pode ser o início de transição ecológica. Essas transições podem ocorrer dependendo de várias condições, como a intensidade e severidade do fogo, e tempo de fechamento do dossel. A queima da vegetação torna a floresta ainda mais inflamável e mais propensa a queimar novamente (Cochrane et al. 1999) e aliado a proximidade de estradas e áreas desmatadas e de exploração madeireira favorecem a chegada de propágulos de espécies invasoras exóticas constantemente, aumentando a degradação e promovendo a inflamabilidade que exclui espécies florestais, diminuindo a resiliência e instalando novos sistemas de *feebacks* que mantem o sistema e outros estados alternativos a floresta (Bond e Midgley 1995; Flores, 2016).

Porém, ainda existe muito trabalho científico a ser realizado para quantificar os vetores de degradação florestal, bem como suas sinergias. As mudanças climáticas aliadas aos incêndios florestais durante as secas serão um crescente fluxo de perda de carbono florestal. Dois

tipos de ferramentas tornaram-se de grande importância para o estudo dos *feedbacks* do sistema terrestre. Em primeiro lugar estão os modelos baseados em processos que incluem *feedbacks*, os quais ajudam a gerar hipóteses sobre os mecanismos que controlam a dinâmica do sistema. Em segundo lugar estão os dados de satélite que fornecem informações em grande escala que podem ser usadas para confirmar ou refutar as saídas dos modelos. Associar técnicas de modelagem a dados de sensoriamento remoto são esforços para compreender e generalizar vetores de degradação florestal. O desenvolvimento desses modelos ajuda a prever os padrões de empobrecimento da floresta em escalas maiores, além de prover uma excepcional oportunidade para investigar futuras trajetórias de vulnerabilidade da floresta. Ademais, incorporar projeções de mudanças climáticas a estes modelos contribui para o planejamento, decisão e formulação de políticas de mitigação e adaptação.

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